PAPERS IN AVIAN PALEONTOLOGY

HONORING PIERCE BRODKORB

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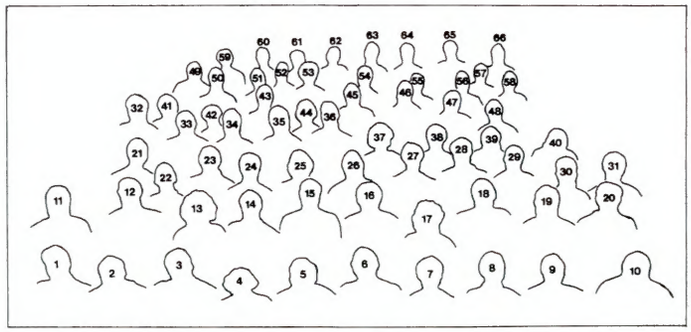
II International Symposium of the Society of Avian Paleontology and Evolution
Natural History Museum of Los Angeles County
Los Angeles, California, USA
28–30 September 1988



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HONORING PIERCE BRODKORB

EDITED BY
KENNETH E. CAMPBELL, JR.

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of the Society of Avian Paleontology and Evolution
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FOREWORD

It is with great personal pleasure that the Natural History Museum of Los Angeles County dedicates this volume of papers on avian paleobiology to Pierce Brodkorb. I first met Pierce in 1953 at a time when I was a premed student just being introduced to vertebrate paleontology through an undergraduate honors project at Amherst College. Later, in 1957 or 1958, I again met Pierce in Hibbie's [Claude W. Hibbard] infamous field camp in Meade County, Kansas. Over the past thirty-some years our friendship has grown as has my respect for Pierce's many accomplishments. Avian paleontology owes him a great debt for his collecting, his teaching, and his research. Dedication of this volume to Pierce Brodkorb is truly deserved.

Dr. Craig C. Black
Director
Natural History Museum of
Los Angeles County

PREFACE

The II International Symposium of the Society of Avian Paleontology and Evolution (SAPE) was held at the Natural History Museum of Los Angeles County, 28–30 September 1988. There was no central theme to the II International SAPE Symposium other than the broad arena of avian evolution. Several papers were presented that described new taxa and new paleoavifaunas, and these are grouped in this volume by geologic age. Other papers discussed various aspects of avian structure, form, and functional morphology. A third group comprised papers that are best grouped as regional surveys because they covered wide geographic areas or several time periods. Papers submitted by those unable to attend the symposium also fall into the preceding categories. Although grouped into tidy categories, the diversity of the papers attests to the variety of approaches avian paleontologists are taking to the study of avian evolution. Taken together, the 38 scientific papers in this volume make a very forceful statement regarding the importance of avian paleontology to studies of avian biology. The members of the SAPE encourage others to join them in this exciting subdiscipline of ornithology.

Pierce Brodkorb, who has contributed so much to the development of avian paleontology and the SAPE, celebrated his 80th birthday on 29 September 1988, the second day of the symposium. The timing of the two events was not entirely coincidental, although until the birthday cake arrived Pierce assumed that they were. (We know this because of the subtle hints he was dropping about it being his birthday!)

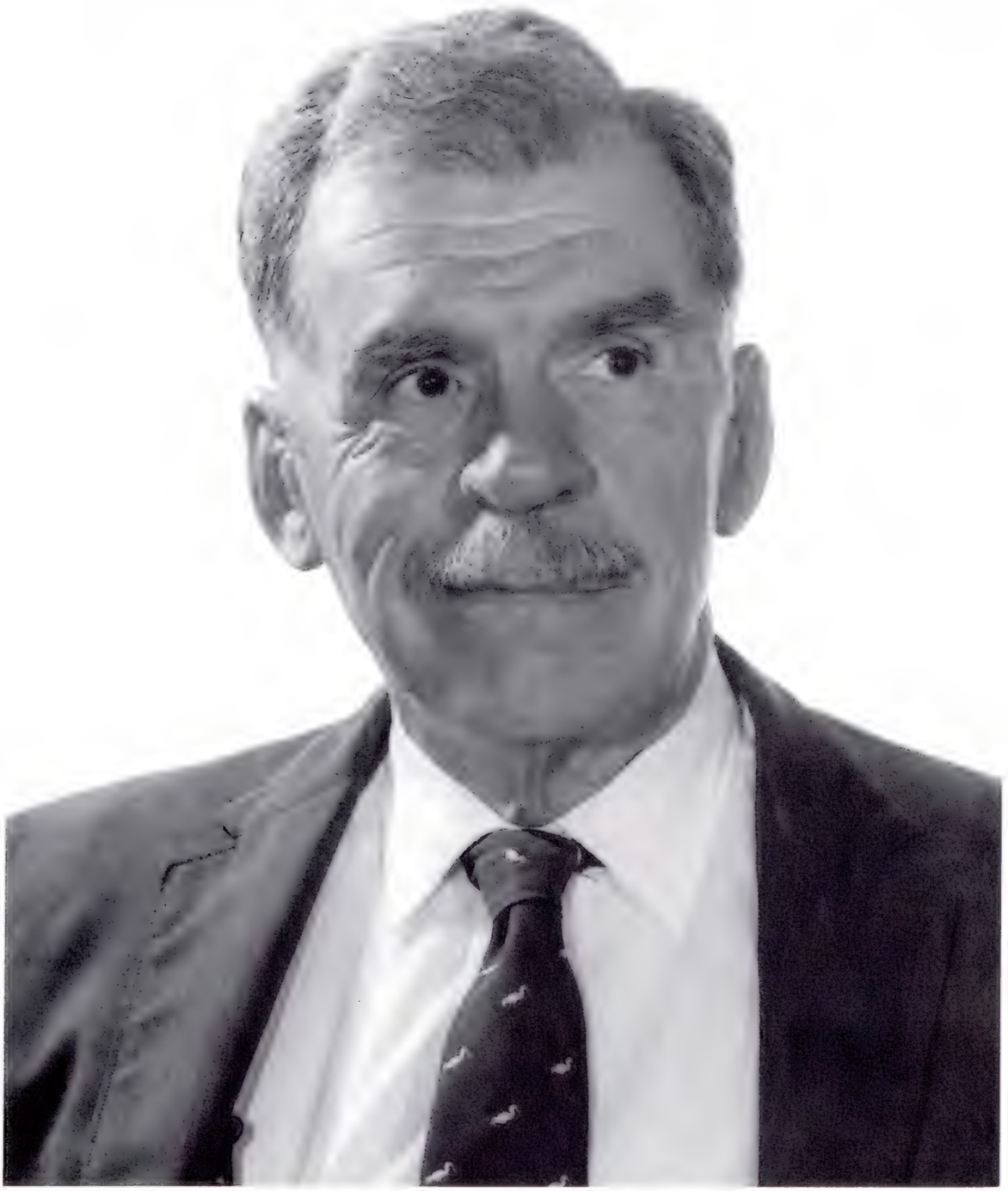
Not all of the papers in this volume were presented at the SAPE symposium; contributions were invited from those unable to attend the symposium, but who wished to join in honoring Pierce Brodkorb. Pierce has had an inordinate impact upon avian paleontology, not only through his published works but, even more importantly, as a kind, stern, loyal mentor and friend who guided so many students into the field. For all he has done for us, we dedicate this volume to Pierce Brodkorb.

The SAPE is an informal international society of persons working on fossil birds, bird evolution, and related problems in avian biology. Current membership comprises almost 175 individuals from over 30 countries. The SAPE was formed in 1985, in Lyon, France, in the course of the "Table Ronde l'Évolution des Oiseaux d'après le témoignage des fossiles," coordinated by Dr. Cécile Mourer-Chauviré, Secretary of the SAPE. Avian paleontologists remain the most active members of the SAPE, but it is hoped that a wider representation of persons working on problems in avian evolution will attend the III International Symposium, to be held at the Forschungsinstitut Senckenberg, Frankfort am Mein, Germany, in 1992, with Dr. D. Stefan Peters as Coordinator.

The editor expresses his appreciation to Dr. Craig C. Black, Director, Natural History Museum of Los Angeles County, for the moral and financial support that made the II International Symposium of the SAPE and the publication of this volume possible, and to the contributors and reviewers who have worked so hard to make this volume a worthy tribute to the lifelong labors of Pierce Brodkorb. I am especially grateful to D.W. Johnston, D. Matthiesen, C. Mourer-Chauviré, C.W. Sibley, D.W. Steadman, R.W. Storer, and G.E. Woolfenden for their assistance with the biography of Pierce Brodkorb. The frontispiece photograph was printed by Richard Meier.

Kenneth E. Campbell, Jr.

DEDICATION



PIERCE BRODKORB: A BIOGRAPHICAL SKETCH

Kenneth E. Campbell, Jr.

When his mother found an English Sparrow in the pocket of four-year-old Pierce Brodkorb's pants, she probably thought he was behaving like any normal child picking up everything in sight. He had, in fact, already chosen his life's work. Now well into his eighties, Pierce Brodkorb is still collecting dead birds, and birds remain as fascinating to him now as when he first became conscious of them. Pierce Brodkorb has not merely studied birds as a career choice—he has lived to study birds.

William Pierce Brodkorb was born in Chicago, Illinois, USA, on 29 September 1908, the first child of William Brodkorb and Virginia Pierce. Before he reached school age, his parents moved the family to Evanston, Illinois, a northern suburb of Chicago. Young Brodkorb attended both grammar school and high school in Evanston, and he speaks very highly of the quality of instruction he received there. It must have been a rather remarkable high school because before graduating Brodkorb had taken four years of Latin and three years of Greek and started French and German classes as well. He studied Latin and Greek, he says, because he wanted to understand the scientific names of birds.

There were a number of stuffed birds in the high school zoology classroom that fascinated Brodkorb, but no one could teach him how to put up a skin. He attempted to teach himself taxidermy by borrowing a book from the local library, but he was not particularly successful. Seeing an article in the *Chicago Tribune* about the return to the Field Museum of Natural History of a collector, Colin Campbell Sanborn, with a collection of bird skins from Chile, Brodkorb wrote for advice. Sanborn, who also lived in Evanston, took the time to reply to the 16-year-old high school student, and he visited the Brodkorb home to show him how to put up skins. Sanborn continued to provide the crucial professional advice that helped Brodkorb through the important beginning phase of his career, and through him Brodkorb was introduced to ornithology at the Field Museum. Before he finished high school, he had sufficiently impressed the curatorial staff with his efforts that they secured summer employment for him as a staff technician. At the Field Museum, Brodkorb came under the influence of H.B. Conover and C.E. Hellmayr, both of whom provided considerable encouragement and assistance to their enthusiastic pupil.

Brodkorb began his college training at Northwestern University in 1926 but left after two years because it was expensive for him and he was also not particularly happy there. He transferred to the University of Illinois, where he received his A.B. degree in 1930. Getting through college was a remarkable achievement, for Brodkorb's father had died when Pierce was still in high school and there was thus no family support. It must also be remembered that these were the years of the Great Depression.

In 1933, Brodkorb went to the University of Michigan, where he received his Ph.D. degree in 1936. His major professor was Dr. Josselyn Van Tyne; his dissertation was a revision of the flycatcher genus *Empidonax*, entitled *A revision of the genus* Empidonax *Cabanis*. After receiving his degree, Brodkorb continued on as Assistant Curator of Birds at the Museum of Zoology at Michigan until 1946, with time out for military service. As Brodkorb relates it, however, Van Tyne was a very difficult person, and strong animosities developed between the two men. Brodkorb cites these disagreeable times as being one of the factors that made entry into the Army Air Force during World War II a far more pleasant experience than it would have been otherwise.

Brodkorb served in the Army Air Force from 1943 to 1946, entering as a 1st Lieutenant. He ended his military service at the grade of Captain, achieving this rank after being recalled for a short period of service after the war. During the war, Brodkorb's mission was establishing and running high-altitude training programs at various air bases around the country, a task he assumed was somehow related to his experiences at high altitude while mountain climbing in search of birds. In these training sessions, flight crews were placed in chambers where they were subjected to increasingly lower levels of oxygen in an attempt to acclimate them to low levels of oxygen. The acclimatization aspect of the program did not work, of course, and no one ever thanked Brodkorb for allowing him to pass out for lack of oxygen, but it was unquestionably good training for the flight crews. One of the bases where Brodkorb was stationed was in Tampa, where he received his introduction to Florida.

It was somewhat ironic that Brodkorb served in the Army Air Force during the war. When he was an undergraduate, he had to participate in the Reserve Officers' Training Corps (R.O.T.C.); the branch he was enrolled in was the cavalry. He says it was more fun galloping a horse across a field, waving a sword, than it was marching. In these years, Brodkorb became quite an expert horseman.

Pierce Brodkorb (right) and Norman Hartweg in Chiapas, Mexico, during a Museum of Zoology, University of Michigan, collecting expedition in 1936.

After World War II, Brodkorb returned to the University of Michigan, but lingering animosities between him and Van Tyne flared. According to Brodkorb, Van Tyne was maneuvering to have him fired when he accepted a position in the Department of Biological Sciences at the University of Florida, a move that he claimed was the best thing that ever happened to him. He hated northern winters.

After receiving his B.A., Brodkorb spent two years, 1931–1932, in the field collecting in Idaho for Harry C. Oberholser of the Cleveland Museum of Natural History. Later, while at the University of Michigan, he collected in the Black Hills of South Dakota in 1935 and in Mexico in 1937, 1939, and 1941; he later returned to Mexico in 1953 when at the University of Florida. His collecting in Mexico was primarily in the State of Chiapas, where he located his base camps after becoming acquainted with a landowner in Esquintla. Brodkorb trained workers at the *finca* to put up bird skins when he was not there; and thus, he was able to build a sizable collection from the region. He worked out of the *finca* most of the years he traveled to Mexico.

It was during his 1939 trip to Mexico that Brodkorb had one of his most harrowing experiences. As he relates it, while collecting near the town of San Cristóbal de las Casas, he passed through a Chumula Indian village. One of the Chumula men began trailing after Brodkorb, pointing out birds and retrieving them after they had been shot. The two men communicated through sign language because the Chumula did not know Spanish and Brodkorb did not know the Chumula language. After having accumulated all the specimens he wanted, Brodkorb indicated that he was going to return to camp. When Brodkorb began walking away, he was shot in the back and neck. Fortunately, the Chumula was only carrying an old muzzleloader, so he was unable to fire again before Brodkorb turned and returned fire. The Chumula fled into the forest and Brodkorb struggled back to town. There he had to wait several hours for medical attention because a doctor could not be found; it was Good Friday and everything was closed. Wounded by large shot pellets (Pierce says they felt more like rusty nails!) in the left shoulder and behind the left ear, it was not a pleasant time, and he still carries the scars from the removal of the shot. Shortly thereafter, Brodkorb lost much of his vision in his right eye, which he attributed to the incident.

Brodkorb assumed a position as Assistant Professor in Biological Sciences at the University of Florida in 1946. He remained there until his retirement on 22 December 1989, completing 43 years of academic service at the university. He became Associate Professor in 1950 and Professor of Zoology in 1955. In his early years at Florida, Brodkorb gradually shifted his interest away from collecting birds for their skins in favor of building up a skeletal collection. In the 1950s and 1960s, Brodkorb spent considerable time in the field collecting fossil birds, which had become the focus of his research. He greatly enjoyed collecting fossil birds and, following the lead of his good friend Claude W. Hibbard, whom he met when both were at the University of Michigan, he collected most of his fossil materials by wet screening. Unlike Hibbard, however, Brodkorb did not do his washing in the field; he carried the matrix back to campus and washed it outside Flint Hall. This kept him in trouble with the groundskeepers, who then had to deal with the lakes of mud he left behind. The major Florida sites he worked were Thomas Farm (Miocene), Bone Valley (Pliocene), and Reddick, Haile, and Arredondo (Pleistocene). He also collected Pleistocene fossils on the island of Bermuda.

In his years as a professor at the University of Florida, Dr. Brodkorb directed to completion 18 master's students and 18 doctoral students. The theses and dissertations completed may be grouped as anatomy, osteology, and physiology (seven M.S., five Ph.D.), comparative studies of living birds (five M.S., four Ph.D.), general fossil vertebrates (one M.S., one Ph.D.), and fossil birds (five M.S., eight Ph.D.). As a graduate student advisor, Brodkorb was not one who made demands on his students. He let them take the lead in their research, and he left them to their own drive to succeed. He provided immense support in securing teaching and research assistantships, writing grant proposals, and easing bureaucratic obstacles. What he did not do was baby-sit. Acting from his own experiences, he firmly believed that students were there because they wanted to learn. He felt his task was to provide the opportunity and leadership by example; students were left to themselves to take advantage of their graduate opportunities. And when they did, he respected his students' endeavors by never assuming coauthorship of a student's research.

Brodkorb served as editor of the *Quarterly Journal of the Florida Academy of Sciences* from 1963 to 1972. In addition to serving as formal reviewer for many journals, publishing houses, and granting agencies, he has for many decades served as informal reviewer of research proposals and paleornithological literature while still in manuscript form. His contributions to ornithological literature and research have thus extended far beyond his own writings, as voluminous and important as they are. He has also served as consultant to the Florida Geological Survey, the British Broadcasting Corporation, and the government of Bermuda. He has been a longtime member of the International Committee on Avian Anatomical Nomenclature.

Dr. Brodkorb has received many awards for his long service to the University of Florida and to ornithology. Most valued among these are the University of Florida Presidential Medallion, in recognition of his many years of service to the University, and the Brewster Medal of the American Ornithologists' Union (A.O.U.) for his outstanding contributions to paleornithology. The Florida Academy of Sciences named Brodkorb the Florida Scientist of the Year in 1970. He was awarded the Annual

Pierce took the occasion of the November 1964 meeting of the Society of Vertebrate Paleontology, held at Gainesville, Florida, to meet with four of his former students. Left to right: Glen E. Woolfenden, Ted T. Allen, P.B., Robert D. Weigel, and J. Hill Hamon.

Faculty Research Award by the University of Florida Chapter of the Society of Sigma Xi in 1970, and he was elected an Honorary Member of the Florida Ornithological Society in 1982. In recognition of his scientific contributions, his colleagues have named at least 22 taxa for him, including 6 herein.

The "award" he particularly seems to treasure, however, was a mounted bird he "won" at the 1934 Fifty-second Meeting of the A.O.U. at the Field Museum in Chicago. This particular bird was actually a composite of bits of feathers and other body parts from numerous species of birds, and it was the prize in a contest at the annual dinner to see who, of all A.O.U. members present, could most accurately determine which species were represented in the mount. The event, part of a spoof on what ornithology might be like 50 [*sic*] years hence (in 1983!) at an imaginary centennial meeting of the society, was described in a report of the meeting (*Auk*, 1935:56) as: "Modifications in plumage, also the result of careful breeding, were illustrated by a strange bird which was offered as a prize to the member who was most successful in identifying the various plumages developed in its makeup." Brodkorb was very proud at having taken this prize.

Of all his achievements, Brodkorb is especially pleased with his role in the creation of the Society of Avian Paleontology and Evolution. Although the gathering upon which this volume is based was entitled the II International Symposium of the Society of Avian Paleontology and Evolution, to be technically correct it should perhaps have been the I International Symposium. This is because at the time Dr. Cécile Mourer-Chauviré convened "The Table Ronde l'Évolution des Oiseaux d'après le témoignage des fossiles," in Lyon, France, in 1985 the Society of Avian Paleontology and Evolution did not exist. During the course of the Table Ronde, Brodkorb proposed the formation of a society for avian paleontology. With everyone in agreement, the society was formed and the Table Ronde assumed the distinction of being its first gathering, although the name of the society was not clearly defined until a later date (C. Mourer-Chauviré, pers. comm.).

To interact with Brodkorb on a daily basis is always a pleasure, although there were times as a student when I was not sure how much fun I was having. Pierce is highly opinionated, but usually capable of backing up his views with rigorous arguments, religion and politics excluded. He is absolutely unintimidated by anyone, which probably helped account for some of the more memorable feuds of his career. Blessed with a great sense of humor, Pierce can always be counted on to lighten the tone of any occasion, and stories by, and about, him will entertain us for some time to come. His ability to see the humor in almost any situation has eased difficult times and made good times even better. To share just two small stories:

One afternoon I visited Pierce in his office and found him alone, laughing to himself. When I inquired as to what had prompted his joviality, he replied that he was just releasing some bottled up laughter. It seems that a student worker whose job it was to help put up skeletons had just left after preparing a Turkey Vulture for maceration. Knowing that this student was a bit particular about what kinds of birds she handled, and being afraid she would not want to prepare the vulture, which someone had brought in the previous day, he had told her only the

first half of its name. Thereupon followed a series of comments during the time she worked on the "turkey," his favorite of which was "How could anything that smells this bad taste so good?" And he was trapped into keeping a straight face!

And one cannot absolve Brodkorb of all the blame for his feud with Van Tyne. It appears that at one time some plumbing had to be repaired in the basement of the Museum of Zoology, the pipes of which extended through Van Tyne's office. During the course of the work, Van Tyne complained at great length about the considerable noise to which he was being subjected, but he was regularly assured by the plumbers that the work would soon be finished. After what must have been, to him, an intolerable length of time, he finally went storming down into the basement to confront the plumbers. What did he find, but Pierce Brodkorb, hammer in hand and devilish grin on face, calmly making like a Pileated Woodpecker beating a staccato on a hollow tree trunk.

THE SCIENTIFIC CONTRIBUTIONS

NEORNITHOLOGY

Pierce Brodkorb began publishing when he was in his eighteenth year, recording eight titles before he turned nineteen. Six of these were published in *The Auk*. He has gone on to publish 189 papers over the course of the 65 years since his first publication, including one (coauthored with J. Becker) in this volume. The publications cover the whole gamut of collection-based ornithological literature. A review of the major contributions of Dr. Brodkorb brings several topics and concentrations of effort to the fore, and a summary of these follows. Throughout the remainder of this text, his papers are referred to by a number enclosed in parentheses; the numbers correspond to those found in his bibliography (see Becker, pp. xxi–xxv, this volume).

Dr. Brodkorb began his scholarly career as a neontologist, following in the footsteps of the ornithologists from whom he learned about birds. Stemming from his early interest in birds and his many hours of field observations, his first 36 publications (1926–1930) were primarily distributional notes, descriptions of breeding activities and food choice, bird censuses, and miscellaneous observations. His most technical paper in this group explored geographic variation in *Thinocorus orbignyanus* (29). This was an apprenticeship period, covering the years of his college education, when he was highly influenced by H.B. Conover and C.E. Hellmayr of the Field Museum of Natural History in Chicago.

The following two years saw a significant drop in Dr. Brodkorb's publication rate because of the many months he spent in the field in Idaho collecting birds for the Cleveland Museum of Natural History. However, these years also saw a shift toward more serious, collection-based ornithological work with the description of two new subspecies of living birds (37, 40).

Over the course of the following 20 years, Dr. Brodkorb proposed new names for 1 order, 1 suborder, 1 family, 1 subfamily, 2 genera, 3 species, and 75 subspecies (see Becker, pp. xxi–xxv, this volume) of living birds. Some of these names were proposed to rectify nomenclatural problems (e.g., 40, 44, 85), but the vast majority were applied to previously unrecognized forms of birds. Many of these taxa were based on specimens received from Central and South America (especially Paraguay) by the University of Michigan's Museum of Zoology; many others were obtained through Dr. Brodkorb's own field work in Mexico (especially Chiapas) and Central America.

No attempt is made here to determine the status of all of the names that Dr. Brodkorb proposed, although a random check shows that many of them are still recognized. A number have also been placed into synonymy, which is not unexpected because many of Brodkorb's proposed names were based on samples far smaller than what would be considered adequate today. It was also difficult to travel to see collections at other institutions and, as Brodkorb noted in 1940 (83), approximately 200 new forms were being described each year during that period. As collections around the world grew, as samples increased in size, as geographic coverage increased, and as trends in geographic variation were recognized, many of what were once "valid" forms were seen as individual or geographic variants. This was an important "shake-down" period in avian systematics, a period when the foundations of modern ornithology were being formed. Pierce Brodkorb played an important role in this phase of ornithology, although this role has been increasingly overlooked in recent decades because it has been overshadowed by his work with fossil birds.

Some other papers during this period should be mentioned because of their special interest. These include comprehensive reviews of geographic variation in *Belonopterus chilensis* (46), *Coragyps atratus* (106), and *Tyrannus dominicensis* (113), a revisionary study of the wren *Thryothorus pleurostictus* (95), and a report on a large collection of birds from the Gulf lowlands of southern Mexico (103) that included over 1000 specimens of 226 forms of birds in 58 families. Dr. Brodkorb's first mention in print of fossil birds appears to be in the paper on the Black Vulture (106).

The final year of this phase of Brodkorb's career saw two papers that seemed to signal a shift in his research interests. The first was a report on the number of feathers in some birds (114), which was followed a few years later by another paper on feathers (127). The second was a report on body temperature and breathing in a nighthawk (115). These papers are of note, not only because they concerned topics rarely addressed by ornithologists up to that time, but also because they represented such a radical departure from Brodkorb's previous works. In the first case (114), Brodkorb individually removed with forceps 113,282 contour feathers from 17 birds, a staggeringly tedious and time-consuming task. Could it have been this intimacy with so many feathers that turned his attention to bird bones and thence to fossil birds?

Before he published his first paper on fossil birds (116), Dr. Brodkorb had published 111 papers on Recent birds. Following his first paper on fossil birds, he never, or rarely, looked back, publishing only seven additional papers on living birds. Only three of these could be considered a continuation of his earlier work; one concerned nomenclature (118) and two concerned distributions (126, 167). The other papers included two on anatomy (127, 140) and the highly successful contributions to the two editions of the valuable resource text *Vertebrates of the United States* (134, 166).

PALEORNITHOLOGY

Pierce Brodkorb's first paper on fossil birds, in which he designated 29 type species for genera erected by Kálmán Lambrecht (116), continued his long-standing efforts to resolve problems in nomenclature. Following this transitional paper, which concerned fossil taxa but not fossil specimens, he began describing fossil birds in 1952 (117).

Over the course of the following 40 years, Pierce Brodkorb has proposed names for 1 order, 8 families, 5 subfamilies, 33

genera, and 84 species of fossil birds. As with the names he proposed for neotaxa, these names were proposed to resolve conflicts in nomenclature or for newly recognized forms. As a pioneer in paleornithology, Dr. Brodkorb faced the incredible difficulty of identifying fossil bird bones at a time when avian osteological collections were a rarity, a fact that led him to build one of the largest, and arguably one of the most usable, comparative avian osteology collections in the country. Although the lack of comparative osteological material has eased somewhat in recent years, it still constitutes one of the major obstacles to paleornithological research.

Although interested, of course, in the well-known Mesozoic birds such as *Archaeopteryx*, *Ichthyornis*, and *Hesperornis*, Brodkorb did not personally involve himself in their study. He did at one time have good intentions of doing so, however, keeping the Yale Peabody Museum's specimens of *Ichthyornis* on loan for 20 years before finally accepting the fact that he would never have time to work on them. Instead, he concentrated on Neogene birds. He collected many of his fossil specimens himself, but he was also regularly sent specimens by paleontologists and archaeologists from around the world who would ask him to identify their specimens. If the collections were small, he would try to oblige, but if they were large, such as those from the Talara Tar Seeps of Peru or Olduvai Gorge of Tanzania, he preferred to turn them over to graduate students for their dissertation research.

Two of Dr. Brodkorb's papers did concern Mesozoic birds, however. One of these was the description of three new genera and six new species from the type locality of the Cretaceous Lance Formation of Wyoming (156), which at the time were the first additions to the Mesozoic avifauna in 30 years. The second reported the first land bird to be described from the Cretaceous, *Alexornis antecedens* of Baja California, Mexico (182).

The only Paleogene bird described by Brodkorb was *Primobucco mcgrewi* (173) from the Eocene Green River Formation, the oldest record of the (now) neotropical family Bucconidae and the order Piciformes.

The Lower Miocene Hawthorne Formation at Thomas Farm, Florida, has produced a number of fossil birds (see Becker and Brodkorb, this volume), of which Brodkorb described three species (125, 132). In a later paper (153), he described four new species from sites in the Hawthorne Formation in Gainesville and Tallahassee, Florida. Brodkorb often recounted how he went out to Thomas Farm with his graduate students to collect matrix for screen-washing back in the laboratory ("permanently" stopping up his lab sink in the process before being forced to take this work outdoors). It was his way of demonstrating that bird fossils were far more common than most paleontologists wished to admit. If only they would bother collecting postcranial bones instead of just teeth and skulls, he would lament, we would have a far greater knowledge of the fossil record of birds.

One of the richly fossiliferous deposits in Florida that produced a number of specimens described by Dr. Brodkorb is the phosphatic, marine Pliocene Bone Valley Formation. Three of his early papers on fossil birds (120, 121, 123) described new species from these deposits, and in a major paper (129) a few years later he described specimens of 18 species from this formation, which included 2 new genera and 10 new species. It was in this latter paper that he first began to discuss species turnover rates, a theme he followed up in later papers where he discussed the longevity of avian species and how many species may have existed since the evolution of birds (139, 176).

The Alachua clay of north-central Florida, a temporal terrestrial or freshwater equivalent to the Bone Valley Formation, produced three new species of birds (148) as well as a fossil of a species of cormorant described by Brodkorb from the Bone Valley Formation.

In addition to Pliocene birds from Florida, Brodkorb described paleotaxa of this age from California (122), Idaho (136), Kansas (147, 160, 169), Oregon (135, 144), and South Dakota (157) in the United States and the Omo Basin of Ethiopia (184, 187) and the Olduvai Gorge of Tanzania (187, 188, 190; these three papers in collaboration with Cécile Mourer-Chauviré). These materials were all sent to Brodkorb in the hopes that he would identify them—hopes that he always tried to fulfill.

Many Pleistocene deposits throughout Florida have proven to be very rich in fossil birds, and a species of rail from one of the most productive of these, Reddick, was the first paleotaxon described by Dr. Brodkorb (117). Brodkorb carried out extensive collecting activities at Reddick, amassing a collection of perhaps tens of thousands of avian specimens from the locality (they remain uncounted). He later described a second species of rail (124), a grebe (152), and four species of passerines (133) from the site. The total number of species he reported from Reddick reached 52 (133).

Other Pleistocene sites in Florida from which Brodkorb reported fossil birds were Haile (119), Eichelberger Cave (129), Crystal Springs (131), Arredondo (137; two new genera, five new species), and Santa Fe River (149). The specimens from the latter site, two bones of a phorusracoid he named *Titanus walleri*, were perhaps the most unexpected, and exciting, fossil birds Brodkorb ever described from Florida, both because they were from a giant flightless bird and because they were so interesting from a paleobiogeographic point of view. These birds had never before been recorded outside of southern South America.

Brodkorb also reported on Pleistocene birds from Idaho (155) and Maryland (189) in the United States, the Bahamas (138; six new paleospecies), Barbados (161), Cuba (141, 168), and Mexico (151, 179). I find it interesting that in his discussion of the paleoavifauna of the Bahamas Dr. Brodkorb concluded that land area was a major factor in the diversity of those islands' avifauna, almost a full decade before this hypothesis played an important role in theoretical studies of island biogeography. He was not the first to draw a connection between island surface area and diversity, but he probably arrived at it independently. He was certainly the first to do so on the basis of paleoavifaunas.

Pierce Brodkorb's most famous, and most welcomed, contributions to paleornithology are, of course, his five-part *Catalogue of Fossil Birds* (150, 158, 165, 175, 183). These works have proven invaluable to not only paleornithologists, but also to neornithologists and paleontologists in all fields. A measure of their success and importance was the rapidity with which they always went out of print, and the endless questions as to when he was going to finish the next volume, questions that always drove him to exasperation because they came so often. That Brodkorb was able to put these works together at all is remarkable, considering that he initiated the catalogue before the age of photocopiers and finished it before the age of computers. All who work in ornithology owe Dr. Brodkorb a tremendous debt of gratitude for the enormous amount of time and energy he put into those works.

Many of the names proposed for paleotaxa, or returned to their proper place, by Dr. Brodkorb resulted from his work in sorting out complex problems of zoological nomenclature that had accumulated in a century of work by various, and variously competent, workers that had named fossil birds. This work was

Pierce maintained a rather infamous laboratory in Flint Hall, where he spent many hours working on the preparation of skeletons for his osteology collection. The year is 1968.

certainly facilitated by Dr. Brodkorb's training as a classical scholar, but it was nonetheless a herculean task. As mentioned earlier, his first paper devoted to fossil birds (116) falls into this category, as do a number published later (142, 145, 146, 154, 159, 160, 163, 170, 171, 174, 184). Not all papers in the latter group were limited to problems of nomenclature; some served as vehicles for the description of new specimens of fossil birds (e.g., 167, 184).

Not everyone has been pleased with the *Catalogue of Fossil Birds*, however. As a strong adherent to the spirit as well as the articles of the International Code of Zoological Nomenclature, Dr. Brodkorb was firm in applying the Law of Priority, the bedrock of the Code, to the use of scientific names, in every instance. Thus, many neornithologists remain upset with his use of Vulturidae (instead of Cathartidae), Plataleidae (instead of Threskiornithidae), Halcyonidae (instead of Alcedinidae), Ardeiformes (instead of Ciconiiformes), Accipitriformes (instead of Falconiformes), and Ralliformes (instead of Gruiformes), among others. This is not to imply that all paleornithologists follow Brodkorb's lead, as can be seen by the exceptions in this volume. Controversy should never be seen as improper in science, and as Brodkorb wrote (166:279), ". . . in my opinion it is more important for students to evaluate revisionary works than blindly to follow static authority." He certainly would not wish to be viewed as a "static authority."

THE BRODKORB COLLECTION

Brodkorb is a collection-based ornithologist. Over the course of his several decades of professional activities, he amassed the largest private collection of avian specimens in the country, comprising both modern and fossil birds. His collections were his pride and joy, his working library, and he worked assiduously to bring together as wide a representation of birds from around the world as possible. He did his own field collecting, gladly accepted any bird brought to him by members of the community, and he never passed up a road kill. He supported graduate students in the field in exchange for specimens, hired people to collect for him, and traded specimens. And his collections were very carefully curated. Students were always welcome to work with the collections, but woe unto them that picked up a bird skin the wrong way, or upset the order of his skeletons, or fleshed out a bird for its skeleton using a scalpel—which might nick a bone.

Brodkorb firmly considered individual specimens to be the true basis of ornithology, and he always insisted that there was no unimportant specimen. In this he led by example, putting in long hours in the preparation and curation of his specimens. If he had what he considered to be an adequate series of a species, he would put up another specimen of that species anyway, using it for trade or, often, donating it to the Florida Museum of

Natural History. Of course, there were those who, for olfactory reasons, wished he had not been quite so taken with macerating birds.

Brodkorb did not seriously begin building his private collection until after he joined the faculty at the University of Florida. Prior to this time, the fruits of his collecting labors went to the institutions with which he was affiliated, especially to the Museum of Zoology at the University of Michigan. When Brodkorb was forced to leave the Museum of Zoology, he lost ready access to the large skin collection he had made, the results of over ten years of collecting efforts. He swore he would never let that happen again. This position led him into a long-running conflict with various elements at the University of Florida when the Florida Museum of Natural History (then the Florida State Museum) was formed, based primarily on the collections that had been built up over the years by members of the faculty of the Department of Biological Sciences (now the Department of Zoology). When attempts were made to force incorporation of the Brodkorb Collection into those of the new Florida museum, Brodkorb refused to give up title to his collections, an action that resulted in still legendary campus battles, some of which continued over decades. But they were battles that he won.

In spite of the many conflicts and sometimes lingering animosities, in 1988 Pierce Brodkorb presented the Brodkorb Collection to the Florida Museum of Natural History at the University of Florida. I think Pierce always intended to present his collections to the University of Florida, but only when he was ready. He may have had difficulties with individuals over the years, but he loved his university and he was proud of his contributions to making it a great university. By presenting his collections to the University of Florida, he has ensured that he will continue contributing to the growth of his university for decades to come.

At the time the collection was presented to the University, it numbered almost 3700 bird skins from 120 families, approximately 12,500 bird skeletons from 129 families, and a still uncounted number of fossil bird specimens that reaches into the tens of thousands.

In summary, Pierce Brodkorb is a consummate ornithologist, born to his life's work. From boyhood bird-watching he progressed through his career to assume a position as a widely respected neornithologist. Completely switching the focus of his research in mid-career, he became a pioneer in the field of paleornithology and went on to world-renown as a dedicated paleontologist. Single-handedly he built what stood for decades as one of the largest collections of avian osteological specimens in the world as well as large skin and fossil collections. He gave freely of his time to students and colleagues, just as a field collector once gave a friendly helping hand to him, and he is responsible for the training received by many of today's active neornithologists and paleornithologists.

Pierce Brodkorb was the guest of honor at the II SAPE symposium banquet. At that time, former students, friends, and colleagues reminisced about how he had influenced their lives. I think the following quote from that evening summarizes best what Pierce Brodkorb represents to so many of us.

> When I first met P.B., as a beginning graduate student at Florida, I walked into his office, shook his hand, and told him I was interested in the evolution of birds. He went into a brief trance, looked out the window for a while, then stared at me and said,
>
> "Have you ever skinned a trogon?"
>
> "No," I replied humbly.
>
> "Well if you ever do, be very careful. The skin's real thin and half the feathers usually fall out."
>
> With that out-of-the-blue bit of wisdom, he handed me a key to his office and said I should start coming in and looking at skeletons whenever I had the time.

Pierce Brodkorb has provided opportunities and encouragement for generations of students and colleagues, both in his laboratory and around the world. We thank him for that and for giving so much to ornithology. We wish him well.

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Jonathan J. Becker

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1927

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1929

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1930

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* Before circulating his reprints, Brodkorb usually wrote a number on them that was supposed to represent its place in his series of publications. Over the years, however, several publications were not numbered, so the numbers he placed on the reprints, placed here within brackets, do not agree with those of the complete publications list. The numbers Brodkorb wrote on his reprints are added here to prevent confusion over their meaning in the future.

1931

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1932

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1933

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1934

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1935

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60. Recent records of some uncommon Michigan birds. Auk 53(4): 455. [8 October] [56]

1937

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1968

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1970

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1978

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1980

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1981

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1992

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INDEX TO AVIAN TAXA PROPOSED BY PIERCE BRODKORB

Jonathan J. Becker

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TYPE SPECIMENS OF AVIAN FOSSILS IN THE BRODKORB COLLECTION

Jonathan J. Becker

INTRODUCTION

The Brodkorb Collection of fossil birds, with 39 holotypes and numerous referred specimens, is one of the major resources for research in avian paleontology in North America. It is especially rich in material from the Pleistocene of Florida. The following catalogue lists author; bibliographic reference; type material (holotypes and paratypes); geologic age (North American Land Mammal Age), if known; and epochs, formation, local fauna, county, and state. Taxonomic arrangement follows Brodkorb's *Catalogue of Fossil Birds* (1963a, 1964, 1967, 1971, 1978), with the genera and species being listed as originally described. In the cases where the taxonomic status of a species has changed from that proposed in its original descriptions, I have summarized the published literature in a short comments section under each species. I have included only the proposals that gave some evidence to substantiate the suggested changes. I have not re-evaluated these controversial species based on the actual examination of the holotype and other relevant material. Also in this section I have noted if a generic name is based on the species. Webb and Patton (1974) provide a partial list of avian types in the Vertebrate Paleontology collections of the Florida Museum of Natural History that is useful in conjunction with this paper.

In November 1988, Pierce Brodkorb donated his collections of fossil and Recent birds to the University of Florida. They are to be housed with the respective collections of the Florida Museum of Natural History, and future inquiries regarding the Brodkorb Collection should be addressed to the curators of those collections.

The treatment herein of specimens that were listed in the original description as "referred material" merits a brief comment. Some students of avian paleontology consider "referred material" to be part of the type series (i.e., paratypes), although they were not designated as such by the original author. This practice follows Recommendation 73D of the International Commission on Zoological Nomenclature (1964), which calls for all specimens other than the holotype listed in the original description to be known as paratypes. For example, Howard (1972), in her catalogue of fossil avian types in the Natural History Museum of Los Angeles County, indicated this by using the term in quotes ("paratypes") to refer to all material cited in the original description, other than the holotype, unless the original author explicitly designated paratypes.

This matter has since been clarified by the International Commission on Zoological Nomenclature (1985). The catalogue that follows is in strict adherence to Article 72(b) of the International Code of Zoological Nomenclature (1985), which states in part "if an author in establishing a nominal species-group taxon nominates . . . a holotype and paratype . . . also lists other specimens, the separate mention of the latter expressly excludes them from the type series." The following section lists material in the same fashion as did the original author, with all non-type material placed under the heading of "Referred material."

Many species from the Pleistocene that are listed in the following section were described from sands and clays filling fissures or caves in the Ocala limestones. The sediments were regarded as distinct formations and were assigned to a glacial or interglacial interval based mainly on the elevation of the locality and their supposed correlation to marine terraces. Although these methods were standard practice by both geologists and paleontologists at that time, recent work (Opdyke et al., 1984) shows the geology of northern peninsular Florida to be more complex and that the sediments in isolated fissures cannot be correlated by elevation. For species described from these localities, I have assigned each to a North American Land Mammal Age based primarily on Webb (1974) and Kurtén and Anderson (1980). Abbreviations used in this list are (dist.), distal end of; (fig.), figure; (pl.), plate; (frag.), fragment; and (prox.), proximal end of.

CLASS AVES

Order Podicipediformes (Fürbringer 1888)

Family Podicipedidae (Bonaparte 1831)

Podiceps dixi Brodkorb

BRODKORB, 1963d:54, fig. 1.

Holotype, right carpometacarpus (prox.), PB 1113. Reddick local fauna, unnamed sands and clays filling fissures in the Eocene Ocala limestones, Marion County, Florida. Rancholabrean, late Pleistocene.

COMMENTS. Steadman (1984) regards *Podiceps dixi* as a junior synonym of *P. auritus* based on his review of the literature on osteology and systematics of Quaternary grebes of North America.

Podilymbus wetmorei Storer

STORER, 1976:151, fig. 1b, d.

Holotype, left tarsometatarsus, PB 1762. Referred material (tentative), humerus, PB 8005. Reddick local fauna, unnamed sands and clays filling fissures in the Eocene Ocala limestones, Marion County, Florida. Rancholabrean, late Pleistocene.

COMMENTS. Campbell (1980) believes that there is a good possibility that *Podilymbus wetmorei* may have been a resident race of *P. podiceps* in peninsular Florida.

Pliodytes lanquisti Brodkorb

BRODKORB, 1953b:953.

Holotype, right coracoid, PB 299. Bone Valley local fauna, Bone Valley Formation, Polk County, Florida. Late Hemphillian, Late Miocene.

COMMENTS. *Pliodytes lanquisti* is the type species for the genus.

Order Pelecaniformes Sharpe 1891

Family Phalacrocoracidae Bonaparte 1854

Phalacrocorax wetmorei Brodkorb

BRODKORB, 1955:12, pl. 3, figs. 10, 11.

Holotype, right coracoid, PB 530 (figs. 10, 11). Paratype, right coracoid, PB 87; left coracoid, PB 168. Referred material, right coracoids (prox.), PB 95, 312, 314, 315, 531; right coracoids (dist.), PB 94, 179, 180, 181, 316, 532, 602; left coracoid (prox.), PB 602 [*sic*]; left coracoid (dist.), PB 119, 313, 533; right scapulae (prox.), PB 97, 326; left scapulae (prox.), PB 96, 185, 607, 657; right humeri (prox.), PB 99, 144; right humerus (shaft), PB 319; right humeri (dist.), PB 102, 103, 183; left humeri (prox.), PB 98, 182, 317; left humeri (shaft), PB 100, 101; left humeri (dist.), PB 104, 121, 122, 184, 303, 608, 658; right radius (prox.), PB 659; left radii (dist.), PB 325, 534, 660; right ulnae (prox.), PB 105, 189, 190, 320, 321, 535, 536, 537, 603, 619, 620; right ulnae (dist.), PB 186, 187, 621; left ulnae (prox.), PB 106, 124, 169, 188, 322, 538, 604; left ulnae (dist.), PB 323, 324, 539, 540, 605; right carpometacarpi (prox.), PB 541, 618; left carpometacarpi (prox.), PB 125, 327, 617; left carpometacarpi (dist.), PB 328, 542, 606; alar digits, PB 117, 126; right femur, PB 662; right femora (prox.), PB 127, 193, 331; left femora, PB 145, 543, 544; left femora (prox.), PB 191, 192, 661; right tibiotarsi (dist.), PB 108, 109; left tibiotarsus (prox.), 107; left tibiotarsi (dist.), PB 110, 128, 170, 194, 195, 545, 609, 616; right tarsometatarsi (prox.), PB 113, 114, 129, 198; right tarsometatarsi (dist.), PB 131, 199, 334, 335; left tarsometatarsi (prox.), PB 111, 112, 115, 130; left tarsometatarsi (dist.), PB 116, 196, 197, 332, 333; synsacra, PB 118, 329, 615, 656; cervical vertebrae, PB 200, 201, 330, 546, 547, 599, 600. Bone Valley local fauna, Bone Valley Formation, Polk County, Florida. Late Hemphillian, Late Miocene.

Family Sulidae Sharpe 1891

Morus peninsularis Brodkorb

BRODKORB, 1955:8, pl. 1, figs. 1, 4; pl. 2, fig. 7.

Holotype, left coracoid, PB 148 (figs. 1, 4, 7). Paratype left coracoid, PB 613. Referred material, cervical vertebra, PB 614. Bone Valley local fauna, Bone Valley Formation, Polk County, Florida. Late Hemphillian, Late Miocene.

Sula guano Brodkorb

BRODKORB, 1955:9, pl. 1, figs. 2, 5; pl. 2, fig. 8.

Holotype, left coracoid, PB 301 (figs. 2, 5, 8). Referred material, right ulnae (frag.), PB 123, 529; tibiotarsus (dist.), PB 309. Bone Valley local fauna, Bone Valley Formation, Polk County, Florida. Late Hemphillian, Late Miocene.

Sula phosphata Brodkorb

BRODKORB, 1955:11, pl. 1, figs. 3, 6; pl. 2, fig. 9.

Holotype, right coracoid, PB 302 (figs. 3, 6, 9). Paratype, left coracoid (lower), PB 138. Referred material, left coracoids (upper), PB 120, 597. Bone Valley local fauna, Bone Valley Formation, Polk County, Florida. Late Hemphillian, Late Miocene.

Sula universitatis Brodkorb

BRODKORB, 1963c:161, pl. 1, figs. c, d.

Holotype, left carpometacarpus (prox.), PB 8505. Gainesville Creeks, Hawthorn Formation, Alachua County, Florida. Hemingfordian, Early Miocene.

Order Ardeiformes (Wagler 1830)

Family Phoenicopteridae Bonaparte 1831

Phoenicopterus floridanus Brodkorb

BRODKORB, 1953a:1, figs. 1, 2.

Holotype, right tibiotarsus (dist.), PB 147. Referred material, shaft of right tibiotarsus, PB 202, right tarsometatarsi (dist.), PB 146, 300. Bone Valley local fauna, Bone Valley Formation, Polk County, Florida. Late Hemphillian, Late Miocene.

Family Ardeidae Vigors 1825

Ardea polkensis Brodkorb

BRODKORB, 1955:17, pl. 4, figs. 13–15.

Holotype, right tarsometatarsus (prox.), PB 308 (figs. 13–15). Bone Valley local fauna, Bone Valley Formation, Polk County, Florida. Late Hemphillian, Late Miocene.

Palaeophoyx columbiana McCoy

McCOY, 1963:338, fig. 1.

Holotype, right coracoid, PB 32 (fig. 1a, b). Paratype, left coracoid, PB 1886. Referred material, left ulna, PB 1887 (fig. 1c). Itchtucknee River local fauna, undesignated formation, Columbia County, Florida. Rancholabrean, late Pleistocene.

COMMENTS. *Palaeophoyx columbiana* is the type species for the genus. Olson (1974b) studied the preceding material and showed that the holotype and paratype are inseparable in morphology from that of the modern *Botaurus lentiginosus* but were slightly smaller in size. He also showed that the referred ulna is from *Tyto alba* and, thus, placed *P. columbiana* in synonymy with *B. lentiginosus.*

Family Ciconiidae (Gray 1840)

Propelargus olseni Brodkorb

BRODKORB, 1963c:162, pl. 1, figs. e–g.

Holotype, left tarsometatarsus (shaft), PB 8504. Seaboard Airline Railroad local fauna, Torreya Formation, Leon County, Florida. Hemingfordian, Early Miocene.

Order Anseriformes (Wagler 1831)

Family Anatidae Vigors 1825

Anas itchtucknee McCoy

McCOY, 1963:341, fig. 2.

Holotype, left coracoid, PB 8500 (emended to PB 8501; Brodkorb, 1964:223). Itchtucknee River local fauna, undesignated formation, Columbia County, Florida. Rancholabrean, late Pleistocene.

COMMENTS. Campbell (1980) reexamined the holotype and other available material but could not determine the validity of this species.

Bucephala ossivallis Brodkorb

BRODKORB, 1955:19, figs. 16, 17.

Holotype, left coracoid (prox.), PB 172 (figs. 16, 17). Bone Valley local fauna, Bone Valley Formation, Polk County, Florida. Late Hemphillian, Late Miocene.

Order Accipitriformes (Vieillot 1816)

Family Accipitridae (Vieillot 1816)

Genus *Proictinia* Shufeldt 1913

Proictinia floridana Brodkorb

BRODKORB, 1956:368, fig. 2.

Holotype, left tarsometatarsus (dist.), PB 777. Thomas Farm local fauna, unnamed sands and clays filling fissures in the Eocene Ocala limestones, Gilchrist County, Florida. Mid-Hemingfordian, Early Miocene.

COMMENTS. Wetmore (1958) moved this species to *Promilio* Wetmore 1958.

Family Falconidae Vigors 1824

Falco readei Brodkorb

BRODKORB, 1959:274, fig. 1.

Holotype, left tibiotarsus (dist.), PB 1692. Arredondo local fauna, unnamed sands and clays filling fissures in the Eocene Ocala limestones, Alachua County, Florida. Rancholabrean, late Pleistocene.

COMMENTS. Campbell (1980) moved this species to *Milvago* Spix 1824.

Order Galliformes (Temminck 1820)

Family Cracidae Vigors 1825

Boreortalis laesslei Brodkorb

BRODKORB, 1954a:182, fig. 1.

Holotype, right tibiotarsus (dist.), PB 743. Thomas Farm local fauna, unnamed sands and clays filling fissures in the Eocene Ocala limestones, Gilchrist County, Florida. Mid-Hemingfordian, Early Miocene.

COMMENTS. *Boreortalis laesslei* is the type species for the genus.

Family Phasianidae Vigors 1825

Colinus suilium Brodkorb

BRODKORB, 1959:276, figs. 2–8.

Holotype, left humerus, PB 1291 (fig. 2). Paratype, right humerus, PB 757. Referred material, left humeri (prox.), PB 758, 1290, 1292, 1624, 1671, 1673; right humeri (dist.), PB 1672, 1703; sternum, PB 1622 (fig. 3); scapula, PB 1648; right coracoid, PB 1623 (fig. 4), 1629; left coracoids, PB 1294, 1701; right ulna, PB 1625; left ulnae, PB 1324 (fig. 5), 1702; synsacrum, PB 756 (fig. 6); right tibiotarsi, PB 1545 (fig. 7), 1649; left tibiotarsi, PB 1634, 1704; right tarsometatarsus, 1626 (fig. 8); left tarsometatarsus, PB 1647. Arredondo local fauna, unnamed sands and clays filling fissures in the Eocene Ocala limestones, Alachua County, Florida. Rancholabrean, late Pleistocene.

COMMENTS. Holman (1961) considered *Colinus suilium* to be a valid species that was a large temporal representative of *Colinus virginianus.* Steadman (1984) agreed that it was a large temporal form but considers it to be a synonym of *C. virginianus.*

Neortyx peninsularis Holman

HOLMAN, 1961:198, fig. 3a–d.

Holotype, left femur, PB 1224 (fig. 3a, b). Referred material, right coracoid, PB 478 (fig. 3c); right coracoids (frag.), PB 1275, 1974; right ulnae (frag.), PB 935 (fig. 3d), 1229. Reddick local fauna, unnamed sands and clays filling fissures in the Eocene Ocala limestones, Marion County, Florida. Rancholabrean, late Pleistocene.

COMMENTS. *Neortyx peninsularis* is the type species for the genus.

Order Ralliformes (Reichenbach 1852)

Family Rallidae Vigors 1825

Genus *Porzanna* Vieillot 1816

Porzana auffenbergi Brodkorb

BRODKORB, 1954b:103, fig. 1.

Holotype, left humerus, PB 742. Haile IA local fauna, unnamed sands and clays filling fissures in the Eocene Ocala limestones, Alachua County, Florida. Rancholabrean, late Pleistocene.

COMMENTS. Olson (1974a) reexamined the holotype and

considered it to be from a species of *Rallus* Linnaeus 1758. He also suggests that this species, *Rallus auffenbergi*, represents a large temporal form of *Rallus limicola* Vieillot 1819.

Laterallus guti Brodkorb

BRODKORB, 1952:80, fig. 1.

Holotype, left humerus, PB 84. Reddick local fauna, unnamed sands and clays filling fissures in the Eocene Ocala limestones, Alachua County, Florida. Rancholabrean, late Pleistocene.

COMMENTS. Brodkorb (1967) moved this species to *Porzana*, in accordance with his view (Brodkorb, 1957a) of placing all crakes in one genus. Olson (1974a) reexamined the type and other referred material and regards this species to be synonymous with *Laterallus exilis* (Temminck 1831).

Gallinula brodkorbi McCoy

McCOY, 1963:344, fig. 3.

Holotype, right humerus, PB 16. Referred material, right humeri (shaft), PB 17, 1826; right ulna, PB 1807; left carpometacarpus, PB 1825. Itchtucknee River local fauna, undesignated formation, Columbia County, Florida. Rancholabrean, late Pleistocene.

COMMENTS. Olson (1974a) considered *Gallinula brodkorbi* a large temporal representative of *Gallinula chloropus* (Linnaeus 1758) and maintained it as a separate species. Later, he regarded it as a temporal subspecies (Olson, 1977). Pending additional work, Campbell (1980) maintained *G. brodkorbi* as a separate species.

Family Gruidae Vigors 1825

Genus *Probalearica*

Probalearica crataegensis Brodkorb

BRODKORB, 1963c:163, pl. 1, fig. h–l.

Holotype, right tibiotarsus (dist.), PB 8503. Seaboard Airline Railroad local fauna, Torreya Formation, Leon County, Florida. Hemingfordian, Early Miocene.

Order Charadriiformes (Huxley 1867)

Charadriidae (Vigors 1825)

Dorypaltus prosphatus Brodkorb

BRODKORB, 1959:281, fig. 9.

Holotype, left humerus (dist.), PB 1712. Referred material, right humerus (prox.), PB 1713. Arredondo local fauna, unnamed sands and clays filling fissures in the Eocene Ocala limestones, Alachua County, Florida. Rancholabrean, late Pleistocene.

COMMENTS. *Dorypaltus prosphatus* is the type species for the genus.

Family Scolopacidae Vigors (1825)

Genus *Limosa* Brisson 1760

Limosa ossivallis Brodkorb

BRODKORB, 1967:185.

Holotype, right tibiotarsus (dist.), PB 526. Bone Valley local fauna, Bone Valley Formation, Polk County, Florida. Late Hemphillian, Late Miocene.

Genus *Erolia* Vieillot 1816

Erolia penepusilla Brodkorb

BRODKORB, 1955:23, fig. 21.

Holotype, left humerus, PB 611 (fig. 21). Bone Valley local fauna, Bone Valley Formation, Polk County, Florida. Late Hemphillian, Late Miocene.

COMMENTS. With the synonymy of *Erolia* Vieillot 1816 with *Calidris* Merrem 1804 (American Ornithologists' Union, 1973), this species becomes *Calidris penepusilla*.

Genus *Calidris* Merrem 1804

Calidris pacis Brodkorb

BRODKORB, 1955:22, figs. 19, 20.

Holotype, left humerus (prox.), PB 594 (figs. 19, 20). Bone Valley local fauna, Bone Valley Formation, Polk County, Florida. Late Hemphillian, Late Miocene.

Family Haematopodidae Gray 1840

Genus *Palostralegus*

Palostralegus sulcatus Brodkorb

BRODKORB, 1955:20, fig. 18.

Holotype, right tibiotarsus (dist.), PB 177 (fig. 18). Bone Valley local fauna, Bone Valley Formation, Polk County, Florida. Late Hemphillian, Late Miocene.

COMMENTS. *Palostralegus sulcatus* is the type species for the genus. Olson and Steadman (1979) consider *Palostralegus* to be a synonym of *Haematopus*.

Family Laridae Vigors 1825

Genus *Larus* Linnaeus 1758

Larus elmorei Brodkorb

BRODKORB, 1953c:94, fig. 1.

Holotype, right humerus (dist.), PB 140 (fig. 1). Referred material, left humerus (dist.), PB 176; right coracoid (prox.), PB 134; left carpometacarpus (dist.), PB 178. Bone Valley local fauna, Bone Valley Formation, Polk County, Florida. Late Hemphillian, Late Miocene.

Family Alcidae Vigors 1825

Genus *Uria* Brisson 1760

Uria brodkorbi Howard

HOWARD, 1981:3, figs. 1–4.

Holotype, partial skeleton in 2 slabs, PB 7960 [a+b]. John Manville diatomite quarry near Lompoc, Sisquoc Formation, Santa Barbara County, California. Clarendonian, Late Miocene.

Australca grandis Brodkorb

BRODKORB, 1955:27, figs. 24–29.

Holotype, right coracoid, PB 141 (figs. 24, 25). Referred material, right humeri (prox.), PB 137, 310 (fig. 26); right humeri (dist.), PB 91, 304 (figs. 27, 28), 305, 595; left humeri (prox.), PB 135, 136, 525; left humerus (dist.), PB 173; left radius (dist.), PB 93;

right ulna (prox.), PB 142; left ulnae (dist.), PB 92, 596; right carpometacarpus (dist.), PB 143; left tibiotarsus (dist.), PB 612 (fig. 29). Bone Valley local fauna, Bone Valley Formation, Polk County, Florida. Late Hemphillian, Late Miocene.

COMMENTS. *Australca grandis* is the type species for the genus. The preceding material includes at least two species (Olson, 1985).

Order Strigiformes (Wagler 1830)

Family Strigidae Vigors 1825

Genus *Pulsatrix*

Pulsatrix arredondoi Brodkorb

BRODKORB, 1969:112, fig. 1.

Holotype, left tarsometatarsus, PB 8420 (fig. 1). Caverna Paredones, San Antonio de los Baños, Provincia Habana, Cuba. Pleistocene.

Order Passeriformes (Linnaeus 1758)

Family Hirundinidae Vigors 1825

Genus *Tachycineta* Cabanis 1851

Tachycineta speleodytes Brodkorb

BRODKORB, 1957b:131, pl. 20, figs. 1–9.

Holotype, left humerus, PB 1270 (pl. 20, fig. 5) with associated left ulna PB 1271 (pl. 20, fig. 1) and left radius (prox.) PB 1272 (pl. 20, fig. 2). Paratypes, left humeri, PB 406, 426, 554, 708, 795, 827, 1231, 1232; right humeri, PB 405, 456, 553, 670, 744, 828, 1066, 1178. Referred material, left humeri, PB 411, 588, 748, 754; right humeri, PB 822, 883, 996, 1073, 1124; left humeri (juvenile), PB 217, 218, 219, 221, 408, 409, 410, 412, 427, 555, 576, 691, 749, 942, 991, 1240; right humeri (juvenile), PB 220, 407, 581, 709, 796, 797, 847, 892, 943, 992, 993, 1072, 1090, 1100, 1101, 1129, 1133, 1319; rostrum, PB 423 (fig. 4); left coracoids, PB 214, 216, 413, 987, 1088 (fig. 3), 1528; right coracoids, PB 213, 215, 1529; left ulnae, PB 414, 415, 416, 419, 420, 432, 671, 916, 928, 1271; right ulnae, PB 417, 421, 433, 582, 918, 926, 939, 994, 995; left carpometacarpi, PB 422, 431 (fig. 6), 1089; right carpometacarpi, PB 222, 1099, 1112, 1538, 1542; left femur, PB 1537 (fig. 7); left tibiotarsi, PB 436, 1074, 1087, 1536, 1544 (fig. 8); right tarsometatarsi (juv.), PB 434, 435, 1539 (fig. 9), 1540. Reddick local fauna, unnamed sands and clays filling fissures in the Eocene Ocala limestones, Marion County, Florida. Rancholabrean, late Pleistocene.

Family Corvidae Vigors 1825

Genus *Protocitta*

Protocitta dixi Brodkorb

BRODKORB, 1957b:132, pl. 20, figs. 14–18.

Holotype, left humerus, PB 428 (pl. 20, fig. 15). Paratypes, left humeri (dist.), PB 351, 832; right humerus (dist.), PB 839. Referred material, left coracoids, PB 968, 1372 (fig. 14); left ulna, PB 425 (fig. 18); right carpometacarpus, PB 1030 (fig. 16); left tarsometatarsi (dist.), PB 833, 1245 (fig. 17); right tarsometatarsi, PB 786, 881. Reddick local fauna, unnamed sands and clays filling fissures in the Eocene Ocala limestones, Marion County, Florida. Rancholabrean, late Pleistocene.

COMMENTS. *Protocitta dixi* is the type species for the genus.

Genus *Henocitta*

Henocitta brodkorbi Holman

HOLMAN, 1959:6, pl. 1, figs. 1, 2.

Holotype, left humerus (dist.), PB 2323. Williston local fauna, unnamed sands and clays filling fissures in the Eocene Ocala limestones, Levy County, Florida. Rancholabrean, late Pleistocene.

COMMENTS. *Henocitta brodkorbi* is the type species for the genus.

Family Troglodytidae (Swainson 1832)

Genus *Cistothorus* Cabanis 1850

Cistothorus brevis Brodkorb

BRODKORB, 1957b:133, pl. 20, figs. 10–13.

Holotype, right humerus, PB 788 (pl. 20, fig. 11). Paratypes, left humerus, PB 437; left humeri (dist.), PB 474, 716, 792, 1627; right humerus (prox.), PB 715; right humerus (dist.), PB 1530. Referred material, left coracoid (upper), PB 476 (pl. 20, fig. 13); left coracoid (lower), PB 791; right ulna, PB 790 (pl. 20, fig. 10); left ulna, PB 475; right tibiotarsus, PB 473 (pl. 20, fig. 12); right tibiotarsus (prox.), PB 789; right tibiotarsus (dist.), PB 1525. Reddick local fauna, unnamed sands and clays filling fissures in the Eocene Ocala limestones, Marion County, Florida. Rancholabrean, late Pleistocene.

Family Icteridae (Vigors 1825)

Genus *Cremaster* Brodkorb 1959

Cremaster tytthus Brodkorb

BRODKORB, 1959:284, figs. 10–12.

Holotype, left tibiotarsus (dist.), PB 1663 (fig. 10). Referred material, right humerus, PB 1664 (fig. 11); right femur (dist.), PB 1694 (fig. 12). Arredondo local fauna, unnamed sands and clays filling fissures in the Eocene Ocala limestones, Alachua County, Florida. Rancholabrean, late Pleistocene.

COMMENTS. *Cremaster tytthus* is the type species for the genus.

Pandanaris floridana Brodkorb

BRODKORB, 1957b:134, text-fig. 1.

Holotype, rostrum, PB 294 (text-fig. 1a, c). Referred material, mandibles, PB 293, 233–253 (text and fig. 1b, d). Reddick local fauna, unnamed sands and clays filling fissures in the Eocene Ocala limestones, Marion County, Florida. Rancholabrean, late Pleistocene.

Family Fringillidae Vigors 1825

Genus *Palaeostruthus*

Palaeostruthus eurius Brodkorb

BRODKORB, 1963b:6, pl. III.

Holotype, left tarsometatarsus (dist.), PB 8502 (pl. III). Late Hemphillian, Late Miocene, Alachua Formation, Haile VI local fauna, Alachua County, Florida.

COMMENTS. Steadman (1981) in his reevaluation of *Palaeostruthus hatcheri* states that *P. eurius* should be regarded as "Passeriformes, indeterminate to family and genus" until it is compared with a large number of passeriformes.

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MESOZOIC

BIRDS

A NEW SPECIMEN OF *ARCHAEOPTERYX* FROM THE SOLNHOFEN LIMESTONE

Peter Wellnhofer

ABSTRACT. A new, well-preserved specimen of *Archaeopteryx* from the Upper Jurassic Solnhofen limestone of Bavaria (Germany) is described and figured. It is the sixth skeletal specimen of *Archaeopteryx* after the London, Berlin, Maxberg, Haarlem, and Eichstätt specimens. The new example, introduced here as the "Solnhofen specimen," is the largest of all, about 10 percent larger than the London individual. The skeleton is fairly complete and it is preserved in its natural articulation. Low-angle illumination reveals impressions of the left wing feathers, mainly of their shafts. The osteological characters of the new specimen show close similarities to the other specimens, especially to those of the London specimen. This includes the peculiar tooth morphology and the relative proportions of the limbs. The new specimen can thus be assigned to *Archaeopteryx lithographica* von Meyer. A taxonomic separation of the smallest example, the Eichstätt specimen, as *Jurapteryx recurva* Howgate seems to be unjustified.

KURZFASSUNG. Es wird ein neues, gut erhaltenes Exemplar von *Archaeopteryx* aus den Oberjura-Plattenkalken der Solnhofener Schichten beschrieben und abgebildet. Es ist der sechste Skelettfund eines "Urvogels" nach den Exemplaren von London, Berlin, Maxberg, Haarlem und Eichstätt. Das neue Exemplar, das hier als das "Solnhofener Exemplar" eingeführt wird, ist das grösste von allen, etwa 10% grösser als das Londoner Individuum. Das Skelett ist ziemlich vollständig und blieb in seiner natürlichen Gelenkverbindung. Jedoch fehlen Teile des Schädels, einige Wirbel, beide Carpalbereiche und der grösste Teil der Zehenglieder des linken Fusses. Es ist kein verknöchertes Sternum vorhanden, wohl dagegen ein Fragment der Furcula. Es wird eine relativ steile Orientierung der Pubes angenommen. Die mittleren Metatarsalia sind teilweise verwachsen. Im Streiflicht treten Abdrücke einer Befiederung des linken Flügels hervor. Die osteologischen Merkmale des neuen Exemplares zeigen weitgehende Übereinstimmung mit den anderen, insbesondere dem Londoner Exemplar. Das bezieht sich auch auf die eigentümliche Zahnmorphologie und die relativen Proportionen der Extremitäten. Es kann deshalb der Art *Archaeopteryx lithographica* von Meyer zugeordnet werden. Eine taxonomische Abtrennung des kleinsten, des Eichstätter Exemplares als *Jurapteryx recurva* Howgate, scheint nicht gerechtfertigt zu sein.

Key words: *Archaeopteryx*, Solnhofen, Jurassic, Aves, morphology.

INTRODUCTION

In November 1987, Dr. Günter Viohl of the Jura Museum in Eichstätt, Bavaria, discovered a new "Urvogel" specimen in the private fossil collection of the former mayor of Solnhofen, Friedrich Müller. I inspected the specimen and confirmed that it was a new specimen of *Archaeopteryx* von Meyer 1861, and subsequently I was given permission to take the specimen on loan to the Bavarian State Collection of Paleontology and Historical Geology in Munich for further preparation and study. In March 1988, the specimen was returned to the "Bürgermeister Müller Museum" of the town of Solnhofen, which had become the owner of the specimen; therefore, it can be called the "Solnhofen specimen." It is the sixth skeletal specimen of *Archaeopteryx*, after the London, Berlin, Maxberg, Haarlem, and Eichstätt examples, or the fifth of that genus, if one follows the suggestion of Howgate (1984c, 1985) to separate the smallest one, the Eichstätt specimen, as distinct.

The specimen named by the author as the "Maxberg specimen" (Wellnhofer, 1974), the third *Archaeopteryx* specimen described by Heller (1959), was removed by its owner from the "Museum auf dem Maxberg" near Solnhofen in 1974, after 15 years on display there. To avoid confusion, this specimen is referred to here as the "Maxberg specimen" and should be for at least as long as it is in private possession.

For the history and the peculiarities of the *Archaeopteryx* specimens, readers should refer to some more general publications, such as those by de Beer (1954), Heller (1959), Ostrom (1985), Stephan (1987), Wellnhofer (1974, 1983), and, especially, to the *Proceedings of the International Archaeopteryx Conference*, Eichstätt, 1984, *The Beginnings of Birds* (Hecht et al., 1985). The Eichstätt conference emphasized the significance of *Archaeopteryx* as the oldest known bird, its phylogenetic position, its mode of life, its flight capabilities, the question of the evolution of flight, and the nature of its habitat. The conference has also shown that many of the problems involved are far from solved. Therefore, every new specimen is of scientific importance, especially if it is as well preserved and complete as the new one (Wellnhofer, 1988a, 1988b).

It remains to be determined whether the new specimen confirms or refutes any or all details and interpretations based on the other specimens. The new specimen being the largest known, the question must be asked as to whether the half-sized Eichstätt specimen can still be viewed as a juvenile individual of *Archaeopteryx lithographica* von Meyer 1861, or whether it is a distinct, smaller species or even genus, as suggested by Mayr (1973) and Howgate (1984c, 1985), respectively.

Finally, it must be stated that the *Archaeopteryx* specimens

from the Solnhofen limestone of Bavaria can still be considered as the oldest known birds in the fossil record (Ostrom, 1987, 1991), despite the announcements of geologically older birds (Jensen, 1981; Chatterjee, 1987, 1991) and the claim that the feather imprints of the *Archaeopteryx* fossils were forgeries (Hoyle and Wickramasinghe, 1986).

Unfortunately, exact locality data are not available for the new specimen. According to the collector, the specimen was discovered many years ago. After his initial preparation, carried out in the spring of 1987, he thought the specimen represented *Compsognathus* Wagner 1861 rather than *Archaeopteryx*. It can be assumed that the specimen originated from the upper section of the Solnhofen limestone (Malm zeta 2b, lower Lower Tithonian), because the lower section (Malm zeta 2a) of the series is usually not quarried. The exact horizon is not known, however. Although the specific quarry from which the specimen came is no longer known, it should be located in one of the larger quarry districts, either around Langenaltheim–Solnhofen, or around Eichstätt, on the so-called Altmühl-Alb of the Southern Franconian Jura.

Contrary to previously discovered specimens of *Archaeopteryx*, a counterpart slab was not preserved. Rather, most of the remains of the dark brown bones are preserved on one slab, 39 × 52 cm and 1.5 cm thick. The slab is apparently from the transitional facies of the so-called "Flinz" to "Fäule," the latter being a somewhat softer, marly limestone (de Buisonjé, 1985). The slab is vaulted, or warped, at its center, near where the thoracic region of the specimen lies. Originally, the slab was broken into several pieces. Bone material was lost from along the cracks, such as in the posterior part of the skull, parts of the cervical and dorsal vertebral column, the distal ends of the scapulae, parts of the shafts of the humeri and of the right tibia, and both carpal regions. The distal end of the tail and the distal portion of the left foot were not on the preserved slab and have been lost. The distal caudal series has been restored to its approximate original length. The gaps in the slab were filled with artificial resin.

Further and more detailed preparation was carried out by Ernst Schmieja, senior preparator of the Bavarian State Collection in Munich. This preparation revealed large parts of the left manus skeleton and cleaned the bones of iron oxide incrustations. Mechanical tools and air abrasive techniques were used in this preparation.

The skeleton of the new *Archaeopteryx* specimen is imbedded, lying on its left side. Both wings and legs are stretched out to one side. The neck is sharply bent backward, to such an extreme that the skull lies beneath the dorsal vertebral column. Also, the tail was pulled upward post-mortem, immediately behind the pelvis. This is in contrast to the condition in the London, Berlin, and Eichstätt specimens, where the tail is preserved in a relatively straight line.

The series of gastralia is still in place, indicating that this individual was imbedded in the sediment while it still retained its soft parts. The high, i.e., dorsal, position of these "abdominal ribs" relative to the ventral extremity of the pubes suggests a certain degree of shrinking of the abdomen, possibly a result of mummification on dry land. The abduction of the right hand is 98°, which is similar to that in the Berlin (100°) and Eichstätt (104°) specimens.

GENERAL DESCRIPTION

Class Aves Linnaeus 1758

Subclass Sauriurae Haeckel 1866

Order Archaeopterygiformes Fürbringer 1888

Family Archaeopterygidae Huxley 1872

Genus *Archaeopteryx* von Meyer 1861

Archaeopteryx lithographica von Meyer 1861

Figures 1–19

MATERIAL. Articulated skeleton (Figs. 1, 2) on a slab (39 × 52 cm) of Solnhofen limestone, transition "Flinz" to "Fäule" variety; Bürgermeister Müller Museum, Solnhofen, Bavaria, Germany.

HORIZON AND LOCALITY. Upper Jurassic Solnhofen limestone, early Lower Tithonian, Malm zeta 2b. Exact locality data unknown; from the quarry districts of the Altmühl-Alb, Bavaria.

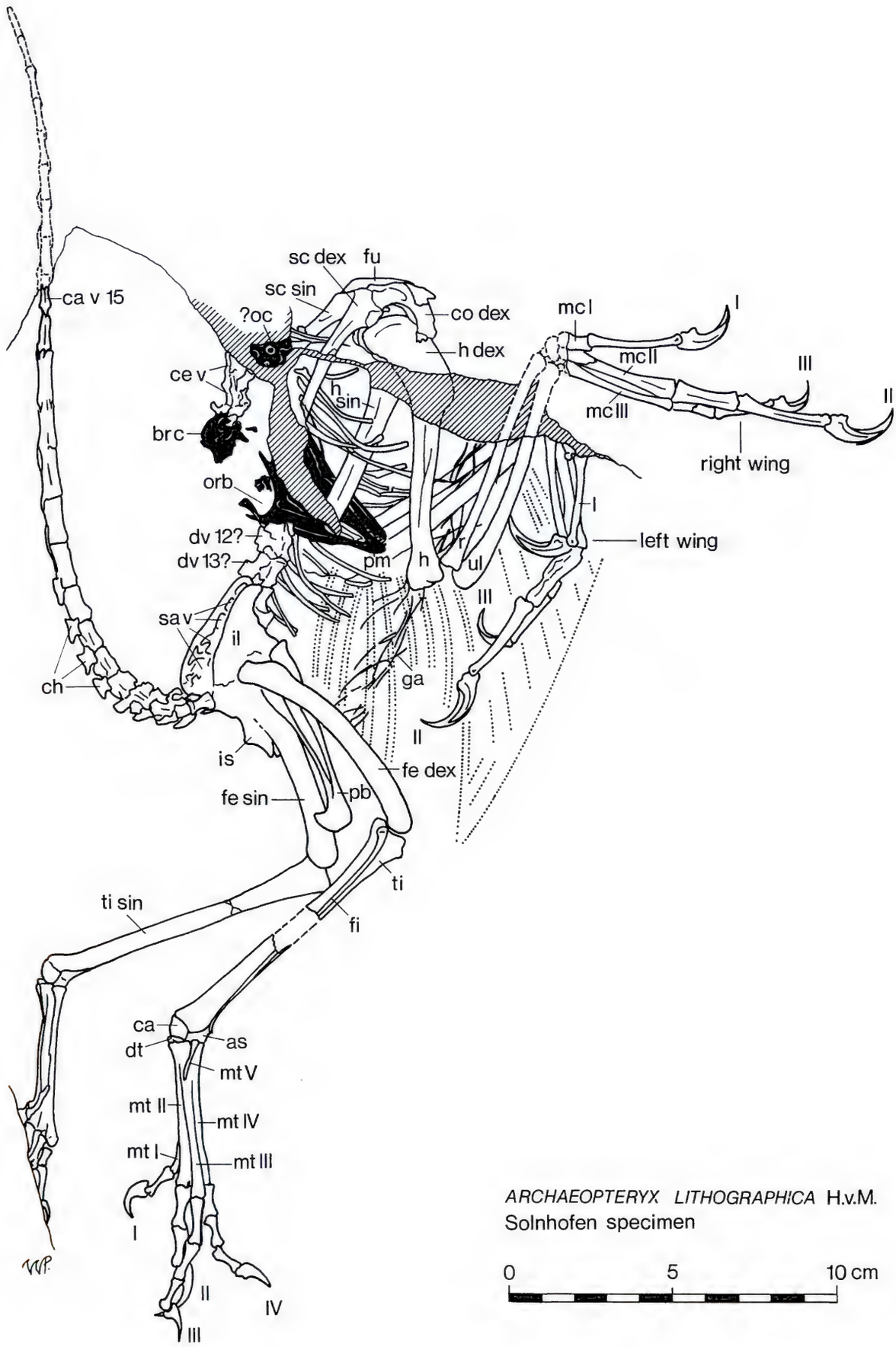
DESCRIPTION. Skull (Figs. 3–6). Only the anterior portion of the skull and mandible, including the premaxilla, maxilla, and dentary, are preserved undistorted. No other skull bones can be identified with certainty because they are badly crushed, dislocated, or missing. The anterior extremity of the left external naris can be recognized, however, as well as the front margin of the left orbit, which can be identified by the presence of some thin bone fragments of the sclerotic ring. The front of the premaxillary is somewhat obtuse and shows a slight depression in its outline, in lateral view, similar to the London specimen.

Four premaxillary teeth and seven maxillary teeth are preserved (Fig. 6). At least one more maxillary tooth should be expected, but the posterior portion of the maxilla is missing. The very tip of the premaxillary is edentulous, followed by one large tooth in vertical position. The following three premaxillary teeth point slightly forward. They show a peculiar constriction in the middle of the crowns (Fig. 6), very similar to the London specimen. The cross-section of the teeth cannot be determined. Between the fourth and fifth tooth, there is a wide gap in which the sharply curved course of the suture between the premaxilla and the maxilla can be observed. The maxillary teeth have mostly broad-based crowns and are directed slightly backward. The second and third become recurved toward their tips; the sixth and seventh are rather blunt.

As in the Berlin and Eichstätt specimens, the mandible is considerably shorter than the upper jaw, leaving the first two premaxillary teeth without a counter bite. Mandibular adduction is so tight that individual mandibular teeth can hardly be distinguished. About six are preserved, partly obscured; approximately five more should have been present in the complete jaw. Posterior skull fragments probably include the frontals, the nasals, the parietals, and the squamosals. Apart from these fragments, a rather solid semicircular bone with a central foramen (foramen magnum?) could be interpreted as the occiput. The distance between the external naris and the front margin of the orbit provides a measure of the size of the skull, which has an estimated length of about 65 mm.

Vertebral Column. A few badly crushed bones in connection with some skull fragments that are interpreted as the parietals are probably a part of the cervical series. Except for a relatively long and low neural spine of one vertebra, which is interpreted as the third cervical, no details can be recognized. Ventral to this vertebra, two short cervical ribs are preserved. Of the dorsal vertebral series, only the last four presacral vertebrae are preserved. On the basis of the vertebral formula of the Eichstätt specimen, they could be the 11th–14th dorsals. If that is correct,

Figure 1. *Archaeopteryx lithographica* von Meyer, the new "Solnhofen specimen," Upper Jurassic Solnhofen limestone, Bavaria. Distal end of the tail has been restored (0.5×). Bürgermeister Müller Museum, Solnhofen.



ARCHAEOPTERYX LITHOGRAPHICA H.v.M.
Solnhofen specimen

0 5 10 cm

the 13th dorsal would be the last dorsal with ribs. Based on the X-ray photographs (Fig. 12B), the dorsals apparently have platycoelous centra. Apparently there are five sacral vertebrae, all of which have rectangular neural spines. The sacrals were connected to the ilia via sacral ribs with broad articular surfaces that contacted the medial surfaces of the ilia.

Fifteen caudal vertebrae are preserved. If 23 caudal vertebrae were originally present, as in the London specimen, then the missing tip of the tail comprised 8 more caudals. These have been restored on the fossil-bearing slab. The caudal centra are clearly procoelous. They increase in length up to the 12th caudal and then decrease in length gradually toward the tip. The well-developed neural spines and the transverse processes of the proximal caudals are reduced distally and disappear from the seventh or eighth caudal onward. The haemapophyses show close similarities with the Eichstätt specimen. Anteriorly they are short and blunt, becoming triangular and plate-like from the fifth caudal onward, and finally elongated, with long anterior and posterior rod-like extensions.

The caudal series becomes twisted at about the 12th and 13th caudal, revealing the dorsal aspect. Both pre- and postzygapophyses have long, rod-like extensions that, together with the haemapophyseal extensions, functioned as a brace for the posterior section of the caudals. As is demonstrated by its position, the tail was flexible mainly at its base.

Ribs. Ten pairs of dorsal ribs are preserved. The three anterior pairs are probably missing, together with their associated vertebrae. The ribs are flattened, proximally rather broad, and, as in the other specimens, without processi uncinati.

Gastralia (Fig. 7). Parallel to the dorsal vertebral column lies a series of gastralia that marks the ventral margin of the abdomen. This suggests that *Archaeopteryx* was imbedded in the sediment with soft parts intact. The gastralia are about 0.5 mm in diameter, taper toward both ends, and are slightly curved. They were originally arranged in sets of three with an angular element in the center and two single elements attached to both ends. How many sets comprised the complete series cannot be determined. The form of the gastralia agrees with that of the other specimens of *Archaeopteryx*.

Shoulder Girdle (Figs. 8, 9). The scapula and coracoid were apparently not fused, as is the case in the London specimen. Both elements were originally in close contact, however, forming the glenoid fossa. At the posterior margin of the exposed right coracoid, a bone is seen from the opposite side, which is interpreted here as the left coracoid.

Scapula: This element is a narrow, long, and distally flattened bone. Dorsally and proximally, a robust acromion is developed, which, according to Ostrom (1976b:12), suggests ". . . that the M. deltoideus was perhaps a more important humeral elevator at the *Archaeopteryx* stage of avian evolution . . ." On the basis of the London specimen, the length of the scapula can be estimated as being 51 mm.

Coracoid: The lateral surface of the right coracoid is exposed. The posterior margin is strongly concave in lateral view, as in the London specimen. The coracoid is a vaulted, broad, bony plate. Its medial part is still imbedded in the sediment. Laterally, below and anterior to the fossa glenoidalis, there is a prominence identified as a "biceps tubercle." According to Ostrom (1976a), this prominence is a homologue of the acrocoracoid in modern carinate birds.

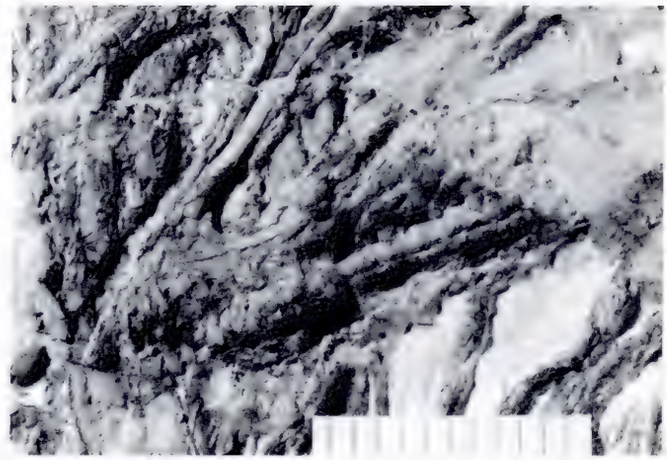


Figure 3. Fragment of the skull of the Solnhofen specimen showing the tip of the snout, including premaxilla, maxilla, external naris, and dentary (3×).

Furcula: Closely appressed to the front of the right coracoid is a slightly curved, obviously flat bone fragment, 25 mm long. This is identified as a ramus of the furcula. It is broken at both ends, however, so that its shape cannot be restored. Ventrally, the break occurs where the element thickens, possibly near the medial symphysis of this normally boomerang-shaped bone (London specimen).

The presence of the furcula in the largest and probably adult individual of *Archaeopteryx* is interesting. I have previously interpreted the missing furcula in the smallest individual, the Eichstätt specimen, as an indication of immaturity (Wellnhofer, 1974).

Sternum: None of the *Archaeopteryx* specimens has as yet revealed any clear evidence of an ossified sternum. The new, and largest, Solnhofen specimen is no exception. Detailed X-ray photographs have revealed nothing that could be identified as a sternum. Therefore, it can be concluded that *Archaeopteryx* probably lacked an ossified sternum.

Wing Skeleton (Figs. 10, 11). Both wings have their natural articulations preserved. The position of the right wing agrees well with the positions shown in the Berlin and Eichstätt specimens. In the left wing, the manus shows a greater flexion at the wrist. Furthermore, the manus is twisted so that the claws point to the body.

Humerus: The right humerus is exposed best. It is a slightly S-shaped, strong bone. Proximally, a wide lateral crest (crista deltopectoralis) is developed. A part of the crest and of the shaft

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Figure 2. *Archaeopteryx lithographica,* the new Solnhofen specimen. The remains of the skull are set off in black. Restored outlines of bones are dashed. Impressions of the feather shafts and the outer margin of the left wing are indicated by dotted lines. Missing parts of the slab are hatched. Abbreviations: **as,** astragalus; **brc,** braincase; **ca,** calcaneum; **ca v,** caudal vertebrae; **ce v,** cervical vertebrae; **ch,** chevrons (haemapophyses); **co,** coracoid; **dex** = right; **dt,** distal tarsals; **dv,** dorsal vertebrae; **fe,** femur; **fi,** fibula; **fu,** furcula; **ga,** gastralia; **h,** humerus; **il,** ilium; **is,** ischium; **mc,** metacarpal; **mt,** metatarsal; **?oc,** ?occiput; **orb,** orbit; **pb,** pubis; **pm,** premaxilla; **r,** radius; **sa v,** sacral vertebrae; **sc,** scapula; **sin** = left; **ti,** tibia; **ul,** ulna.

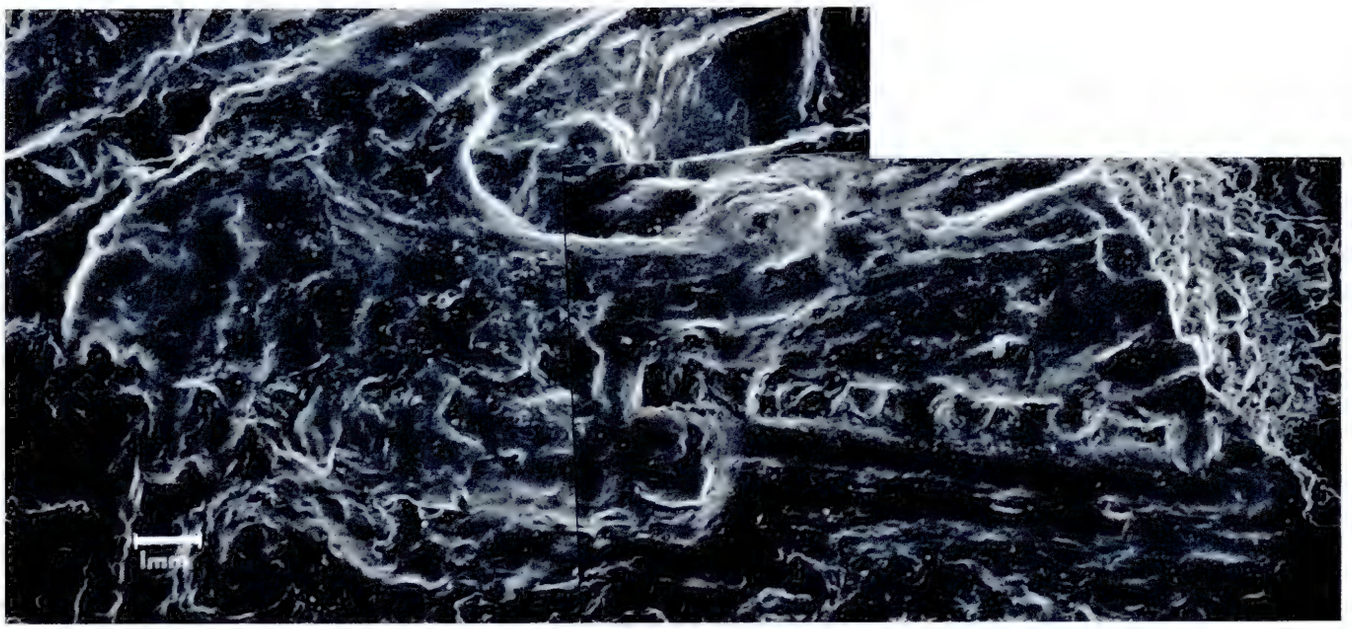


Figure 4. Skull fragment of the Solnhofen specimen showing the dentition. SEM photograph of a cast (Araldit AY 103, Ciba Geigy). Scale bar = 1 mm.

is missing because of a 15-mm-wide gap in the fossil slab. The head is broad and still articulates with the glenoid fossa.

Radius and Ulna: The distal ends are not preserved. Both elements are long, slender bones. The ulna is the stronger, and it is slightly curved, leaving a narrow gap (spatium interosseum) between it and the straight and more slender radius. The ulna is absolutely smooth, without any quill nodes. In this, the specimen agrees with all other specimens of *Archaeopteryx*.

Manus: The wrist area of both wings has been lost. Both metacarpi and the digits are very well preserved, however. The first metacarpal is short, with a well-developed distal trochlea indicating a high degree of flexibility of the first digit. The second

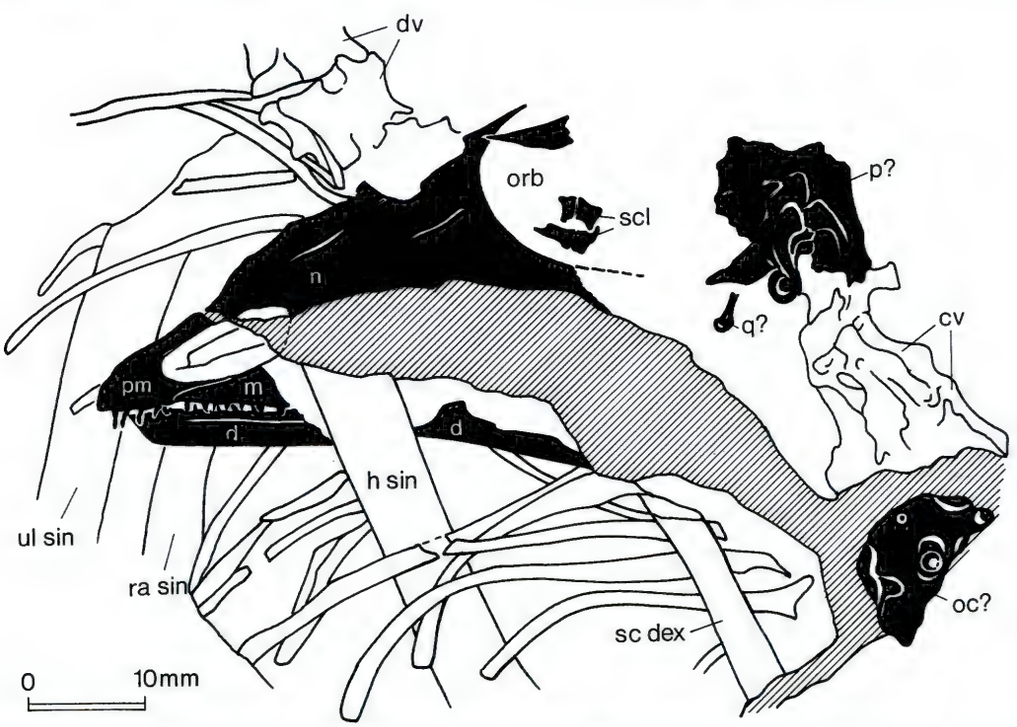


Figure 5. Position of skull elements as preserved in the Solnhofen specimen. Missing parts of the slab are hatched. Abbreviations: **cv,** cervical vertebrae; **d,** dentary; **dv,** dorsal vertebrae; **h sin,** left humerus; **m,** maxilla; **n,** nasal; **oc?,** possible occiput; **orb,** orbit; **p,** parietal; **pm,** premaxilla; **q?,** possible fragment of quadrate; **ra sin,** left radius; **sc dex,** right scapula; **scl,** sclerotic plates; **ul sin,** left ulna.

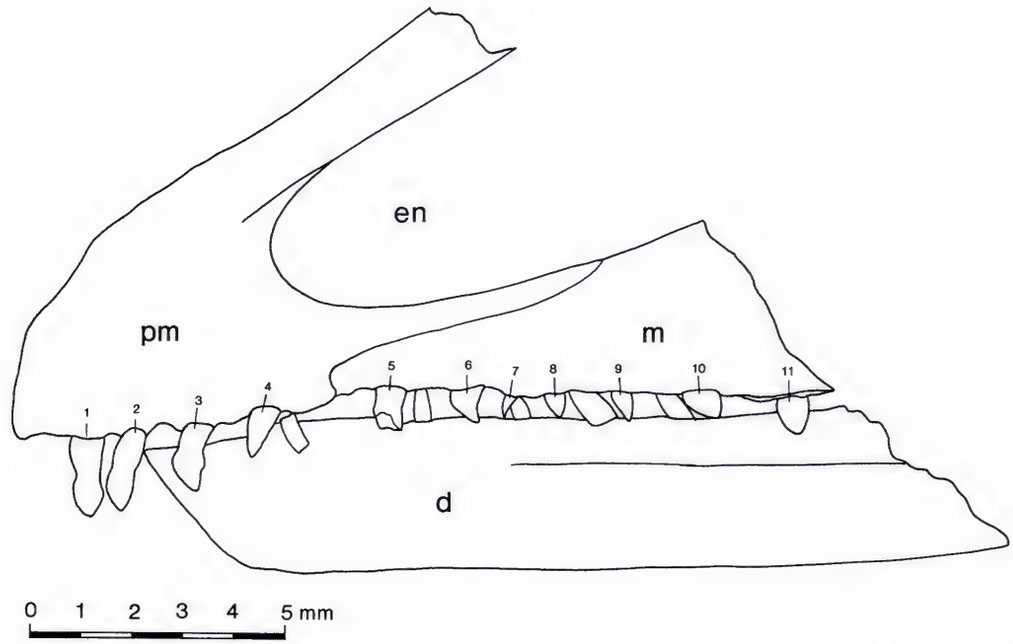


Figure 6. Front end of the snout of the Solnhofen specimen with dentition preserved up to the 11th tooth of the upper jaw. At least one more tooth should have been present in the maxilla. Abbreviations: **d,** dentary; **en,** external naris; **m,** maxilla; **pm,** premaxilla.

and third metacarpals are of about equal length, but the third is considerably more slender and bent.

The digits show the same peculiar position as documented in the Berlin, Eichstätt, and, to a certain degree, the Maxberg specimens. The first digit is flexed anteriorly. The second and third lie closely together, but only up to the penultimate phalanx of the third digit, which then crosses the second digit. The second digit is straight throughout its entire length. Apparently, it was the second digit to which the remiges were attached. The phalangeal formula is 2–3–4, the same as could be demonstrated for the Berlin, Maxberg, and Eichstätt specimens (Wellnhofer, 1985).

Former controversies about the exact number of phalanges in the third digit of *Archaeopteryx* have been settled (Tarsitano and Hecht, 1980; Hecht and Tarsitano, 1982; Thulborn and Hamley, 1982; Howgate, 1984a; Wellnhofer, 1985). The new specimen clearly shows four phalanges in the third digit, and this agrees with the other specimens of *Archaeopteryx*. The first two phalanges are tightly linked, however, and can be distinguished only by an S-shaped suture rather than a well-developed ginglymoid joint, as is shown between the second and third phalanges. The first two phalanges apparently functioned like a single bone. Does this indicate a trend toward fusion of the phalanges of the carpal digits, as occurs in modern birds?

The terminal phalanges of the three carpal digits are strong claws with pronounced flexor tubercles. All claws still retain their horny sheaths, as is clearly shown in ultraviolet light. Morphologically, the finger claws agree in every detail with the claws described in the Eichstätt specimen (Wellnhofer, 1974) and in the Haarlem specimen (Ostrom, 1972). The claws are strongly curved, and the horny sheaths have needle-like tips with a diameter of only 0.3 mm. Yalden (1985) has convincingly demonstrated that these strongly curved and very sharp claws of *Archaeopteryx* were well adapted for climbing on tree trunks. (See Peters and Görgner, this volume.—Ed.)

Pelvis (Figs. 12, 13). The pelvis is compressed but remains in articulation with the vertebral column. The left ilium was shifted dorsad. Only the posterior part of the left ischium is preserved.

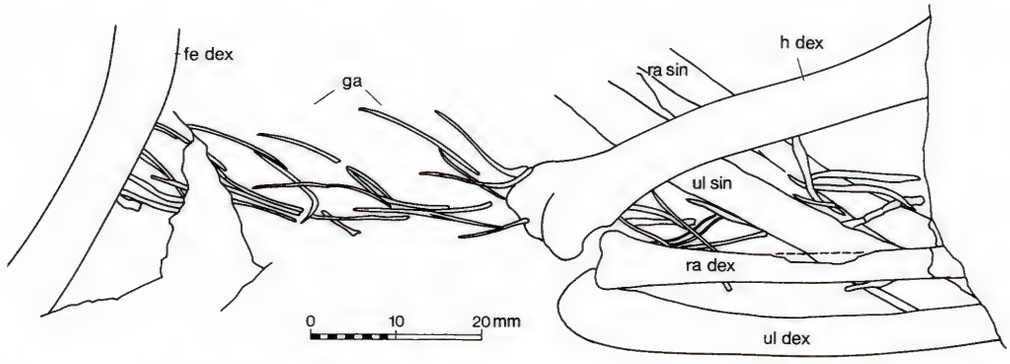


Figure 7. Gastralia as preserved in the Solnhofen specimen. Abbreviations: **fe dex,** right femur; **ga,** gastralia; **h dex,** right humerus; **ra dex,** right radius; **ra sin,** left radius; **ul dex,** right ulna; **ul sin,** left ulna.

Figure 8. Right shoulder articulation of the Solnhofen specimen. Enlarged detail showing both scapulae, the right coracoid, the caput humeri, and a fragment of the furcula (3×). Abbreviations: **co,** coracoid (right); **cr dp,** deltopectoral crest of the right humerus; **fu,** furcula; **h,** humerus (right); **sc,** left (top) and right (below) scapula.

The pubes, fused in a ventral symphysis, were twisted into the bedding plane and therefore do not show their exact original position.

Ilium: The right ilium is exposed in its lateral aspect. The postacetabular part is broken away. As far as the outline can be restored, the shape of the ilium closely resembles the ilium of the London specimen. Anteroventrally, a broad (8 mm) pubic peduncle is present, showing that a distinct facet for articulation with the pubis was present. The acetabulum is circular in outline and has a diameter of 7.5 mm.

Ischium: The posteroventral section of the left ischium is exposed, revealing its medial surface. The posterior and ventral margins show the same characters as the Eichstätt ischium.

Pubis: The right pubis is still in contact with the pubic peduncle of the ilium, although displaced 2 mm anteriad. The contact between the ilium and the pubis obviously was not very firm and may even have been joint-like, allowing the pubis a certain degree of parasagittal movement. This would explain the different pubic orientations in the London, Maxberg, Berlin, and Eichstätt specimens (Wellnhofer, 1985). The long and slender shafts of the pubes are flattened in their middle sections. Originally, they must have met in the midline, as seen in the London specimen. Ventrally, the pubes are co-ossified, forming a hook-like symphysis, the "pubic foot," very similar to the same structure in the other specimens with preserved pubic symphyses.

Orientation of the Pubes. The pubic orientation in *Archaeopteryx* has become a significant character in evaluating its systematic and evolutionary relationships (Tarsitano and Hecht, 1980; Hecht and Tarsitano, 1982; Walker, 1977, 1980; Ostrom, 1972, 1973, 1974, 1975, 1976a; Wellnhofer, 1974, 1985; Howgate, 1985). The question was raised as to whether the pubes were oriented posteriad, and thus bird-like, or ventrad, and thus dinosaur-like. This author (Wellnhofer, 1985) has shown that in all known pelves of *Archaeopteryx,* i.e., in the London, Maxberg, Berlin, and Eichstätt examples, the pubes were more or less dislocated post-mortem (see also Ostrom, 1976a) and do not have their natural orientation. In the new Solnhofen specimen, the left pubis lies at an angle of 120°, and the right pubis at an angle of 132°, to the longitudinal axis of the ilium. If the right pubis is returned to its natural articulation with the pubic peduncle, an angle of 128° results. This is more than the 110° the author estimated on the basis of the other specimens (Wellnhofer, 1985) but less than the 135° of Walker (1980) or the 160° of Tarsitano and Hecht (1980). Howgate (1985:111), however, suggested a "distinctly opisthopubic" condition for the pelvis of the Berlin specimen. He regarded the pubes of the Eichstätt specimen as "almost vertical/slightly opisthopubic," which was one of the reasons he separated the Eichstätt specimen as a distinct genus, *Jurapteryx* Howgate 1985.

As a result of compaction of the sediment, the fork-like, springy pubes were always twisted into the bedding plane post-mortem, thereby losing contact with the ilia. For that reason, the original orientation is difficult to reconstruct. No known specimen of *Archaeopteryx* shows the pubes preserved with an anterior orientation. Instead, all specimens show the pubes oriented more or less posteriad, even the Eichstätt specimen with the steepest pubes. Most likely, therefore, the natural orientation was posterior or opisthopubic, but probably at a fairly steep angle, as all except the Berlin specimen show.

Hindlimbs (Figs. 13–17). The position of the hindlimbs is very similar to that in the Berlin and Eichstätt specimens. They still articulate with the acetabulum and appear rather robust, which was the reason why the skeleton was first taken as a specimen of *Compsognathus,* a small theropod dinosaur from the Solnhofen limestone. The Munich specimen clearly shows a very similar hindlimb arrangement (Ostrom, 1978).

Femur: The femur is a slightly recurved, robust bone. The head is not set off much from the shaft. A massive, rounded "trochanter" is present proximally and anterolaterally.

Tibia: The tibia is 28 percent longer than the femur and straight. An internal cnemial crest is developed proximally and anteriorly.

Fibula: Closely attached to the lateral surface of the right tibia, the right fibula is preserved as a thin, rod-like bone, 0.6–1.0 mm in diameter. It runs the total length of the tibia, from proximolaterally to anterodistally.

Tarsus: Separated by sutures, but tightly connected with the distal extremity of the tibia, two large proximal tarsals can be recognized. The posterior tarsal is interpreted as the calcaneum, which is square in outline. The anterior tarsal is taken to be the astragalus, with an ascending process pressed against the anterior surface of the tibia.

The ascending process of the astragalus in *Archaeopteryx* was interpreted by Ostrom (1976a) as a typical theropod character. Martin et al. (1980), however, regarded this process as a bird-like "pretibial bone," which is fused with the calcaneum in

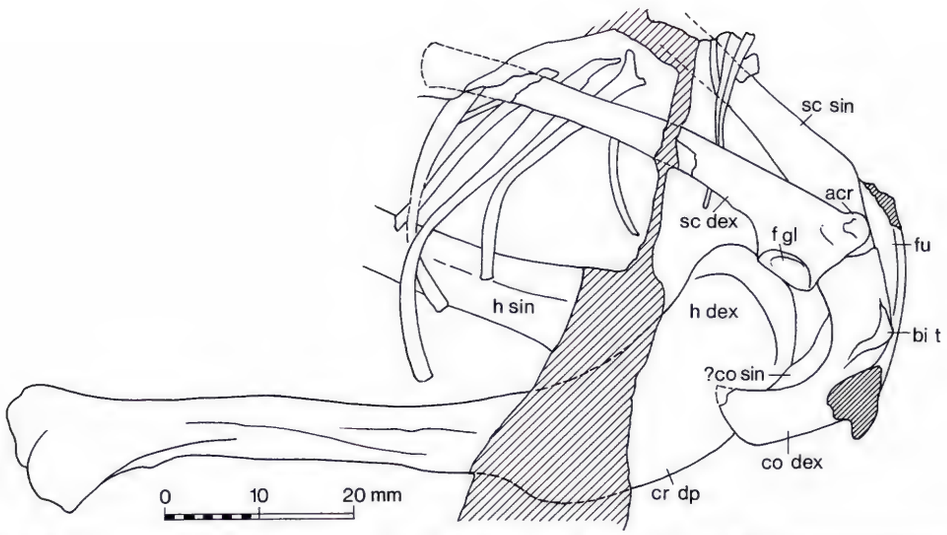


Figure 9. Shoulder girdle as preserved in the Solnhofen specimen. Abbreviations: **acr,** acromion; **bi t,** biceps tubercle of the coracoid; **co dex,** right coracoid; **?co sin,** supposed left coracoid; **cr dp,** deltopectoral crest of the humerus; **f gl,** glenoid fossa; **fu,** furcula; **h dex,** right humerus; **h sin,** left humerus; **sc dex,** right scapula; **sc sin,** left scapula.

modern birds. In the new Solnhofen specimen, as well as in the Eichstätt specimen, a fusion of the process with the calcaneum can be excluded.

In the right foot, two distal tarsals are preserved proximal to metatarsals II and III, but not fused with them. Whether or not a third distal tarsal was present is not clear. The foot has a mesotarsal joint as in the other specimens.

Metatarsus: The three principal metatarsals, II, III, and IV, appear to be rather compact, forming a single functional unit. In the right foot, fusion seems to be possible proximally. In the left foot, metatarsals II and III cannot be clearly distinguished and might be partially fused. The middle metatarsal, III, is the longest. The lateral metatarsals, II and IV, are slightly shorter. The first metatarsal is short and supports the reversed hallux. It presses against the posterior surface of the second metatarsal with its flattened proximal end at about one-third the distance from the distal end of this bone. The first metatarsal has a well-developed proximal articulation, allowing the first, reversed toe a high degree of flexibility.

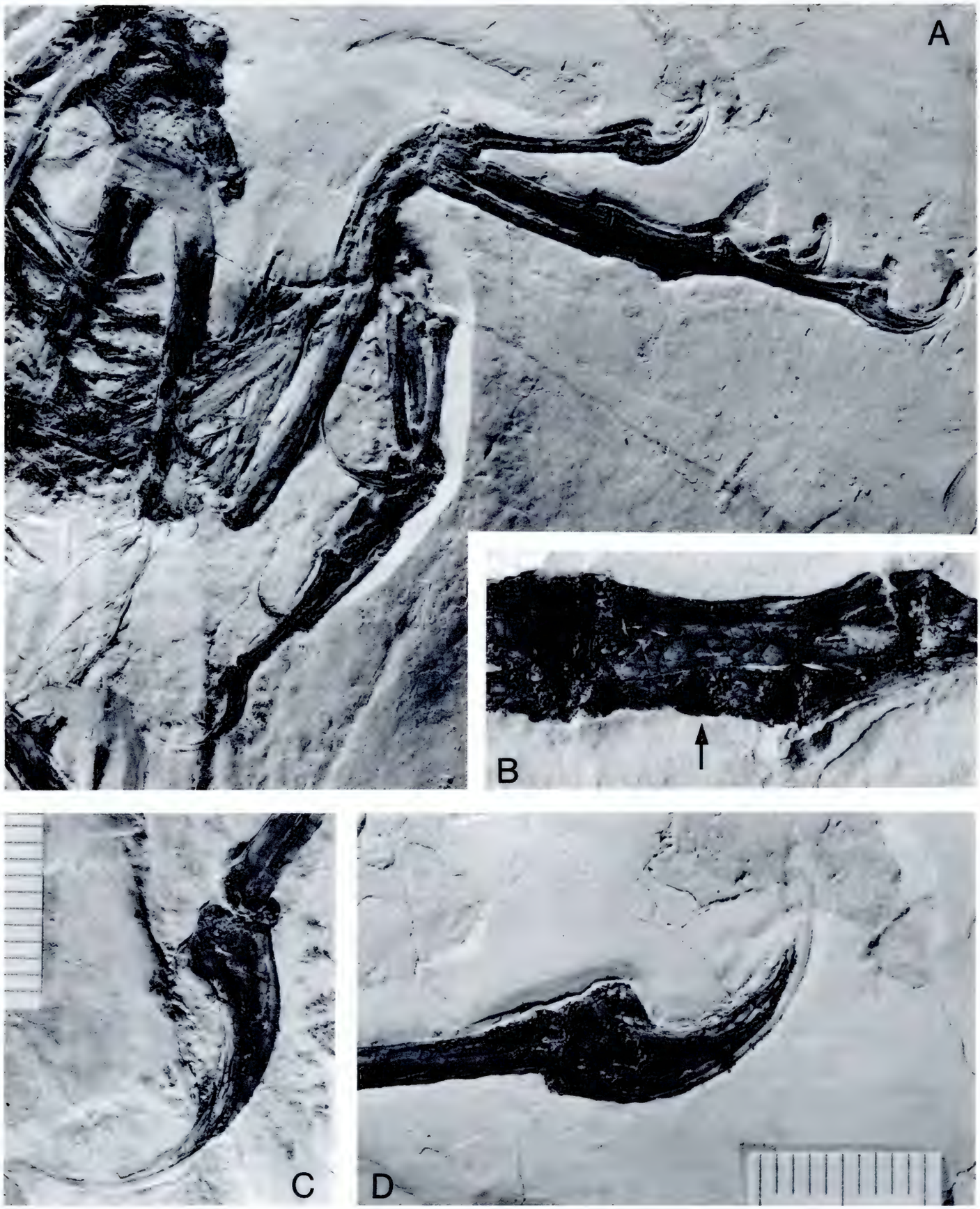
The fifth metatarsal is a delicate, splint-like bone, only 0.5 mm in diameter and 10.5 mm long, lying obliquely over the proximal parts of the metatarsals III and IV. In its shape and position, the fifth metatarsal in the Eichstätt specimen is very similar (Wellnhofer, 1974). It also has a striking similarity with the same element in *Avimimus* Kurzanov 1981, a theropod dinosaur from the Upper Cretaceous of Mongolia (Kurzanov, 1987:fig. 22) and in other theropods (Ostrom, 1976b).

Digits: Only the toes of the right foot are completely preserved. The phalangeal formula reads 2–3–4–4–0, rather than 2–3–4–5–0 as documented in the Berlin and Eichstätt specimens. The fourth digit clearly has only four phalanges, including the claw that still has preserved remnants of its horny sheath. This is quite surprising because this unusual formula is not seen in birds, nor in theropod dinosaurs, nor in thecodonts. Unfortunately, the left foot is incomplete and cannot be used for a counter-check.

It is interesting, however, that de Beer (1954:29) thought that the fourth toe in the London specimen consisted of "presumably four" phalanges. But the fourth toe in that individual is partly hidden by the second toe in such a way that not all of the phalanges of the fourth digit are visible. And again, the opposite foot is not preserved. Only X-ray examination could resolve this question in the London specimen. It is hard to imagine that the London and the new Solnhofen specimens would differ in this character alone from the other specimens, whereas they share so many other similarities. As long as the phalangeal formula of the London specimen is unclear, I prefer to interpret the abnormal count of the phalanges in the fourth toe of the Solnhofen specimen as an anomaly, i.e., hypophalangy.

Feather Imprints (Fig. 18). Recently, several non-paleontologists have speculated that the feather impressions found with the *Archaeopteryx* specimens were forgeries, faked to skeletons of the little theropod *Compsognathus* (Watkins et al., 1985; Hoyle and Wickramasinghe, 1986). Although this "hypothesis" has already been disproved on sound scientific grounds (Charig et al., 1986), one is eager to see whether or not evidence indicates feathers in the new specimen. Indeed, under low-angle illumination, a number of parallel, slightly recurved structures are visible on the surface of the slab in the area between the left lower arm and the right femur. These must be interpreted as the imprints of the shafts of the secondary flight feathers of the left wing. Proximally, eight shaft impressions can clearly be distinguished, and distally six or seven more are visible, although more faint. They were originally attached to the left ulna. This agrees with the suggestion of Stephan (1987) that at least 12, and possibly up to 15, secondary flight feathers were developed in *Archaeopteryx*. The impressions of wing feathers continue beyond the skeleton of the left hand. The wing area is marked by a slight furrow, subparallel to the second digit of the left manus. Detailed feather imprints of the primary feathers of the left wing are not preserved. Neither the right wing nor the tail shows any feather marks. Apparently, the imprints of the feathers of the left wing were preserved because it was lying underneath the body and was thus protected against decomposition.

All six skeletal specimens of *Archaeopteryx* show feather imprints of varying detail. Best detail is documented, of course, in the Berlin and London specimens, but imprints are also present in the Maxberg (Heller, 1959), Haarlem (Ostrom, 1972), and


A
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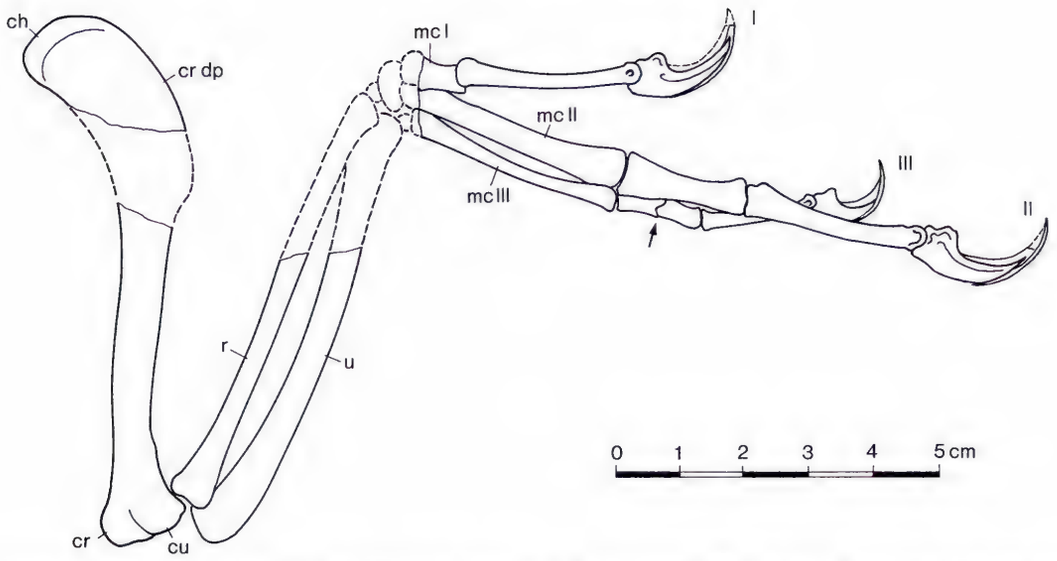

Figure 11. Right wing skeleton as preserved in the Solnhofen specimen, in dorsal aspect. The outlines of missing parts are dashed. The arrow points to the "articulation" separating the first and the second phalanges of the third digit.
Abbreviations: **ch,** caput humeri; **cr,** condylus radialis; **cr dp,** deltopectoral crest of the humerus; **cu,** condylus ulnaris; **mc I, II, III,** metacarpals I, II, and III; **r,** radius; **u,** ulna.

Eichstätt (Wellnhofer, 1974) specimens, as well as the isolated feather (von Meyer, 1861) on the slab and counter slab in Berlin and Munich, respectively.

For a complete set of measurements of the Solnhofen specimen, see Table 1.

COMPARISON OF THE SOLNHOFEN SPECIMEN OF *ARCHAEOPTERYX* WITH THE OTHER SPECIMENS

The new Solnhofen specimen of *Archaeopteryx* is the largest known, with the London, Maxberg, Haarlem, Berlin, and Eichstätt specimens being of respectively smaller size (Table 2). More informative are the ratios presented in Table 3. Based on the length of the humerus, the London specimen is 90 percent, the Maxberg specimen 87 percent, the Berlin specimen 77 percent, and the Eichstätt specimen 50 percent the size of the Solnhofen specimen. Using the length of the entire arm, the Berlin specimen reaches 75 percent the size of the Solnhofen specimen. In other words, the London specimen is 10 percent, the Maxberg specimen 13 percent, the Berlin specimen 25 percent, and the Eichstätt specimen 50 percent smaller than the new Solnhofen specimen. No exact measurements can be taken of the Haarlem specimen; however, Ostrom (1972) suggested a size of 10 percent larger than the Berlin specimen, or about the size of the Maxberg specimen.

A comparison of the humerus length with the lengths of the ulna and of the hand skeleton (mc II + digit II) demonstrates that all specimens have similar proportions. This is not the case when the hindlimbs are compared. The Eichstätt specimen is distinct by having a longer femur, longer tibia, and longer foot (mt III + digit III), increasing in that order. The ratio of the lengths of the wings of the Solnhofen and the Eichstätt specimens is 2:1; however, the ratio of the lengths of the hindlimbs is 1.7:1. Both wing and hindlimb skeleton are about equal in length in the Solnhofen and Berlin specimens, but in the Eichstätt specimen the hindlimb is 16 percent longer than the wing.

A comparative anatomical study of the Solnhofen specimen reveals the following.

SKULL

As in the London, Berlin, and Eichstätt skulls, the premaxilla of the new specimen has an obtuse anterior extremity and bears four teeth (Fig. 19). The premaxillary/maxillary suture is sharply bent, as in the Eichstätt specimen. The premaxillary teeth show a slight but distinct constriction, or "waist," halfway up the crowns, the same as in the London and Berlin specimens (Howgate, 1984b). A reexamination of the teeth of the Eichstätt specimen revealed that its premaxillary teeth are also constricted, although to a lesser degree. The maximum height of the crown of the premaxillary teeth is 1.5 mm in the Solnhofen specimen and 1.1 mm in the London specimen (after Howgate, 1984c). The maximum diameter of the crown of the maxillary teeth is 0.8 mm and, thus, slightly less than in the London specimen where it is 0.9 mm. The lower jaw recedes from the upper jaw, as in the Berlin and Eichstätt specimens, indicating a certain degree of intracranial kinesis.

VERTEBRAL COLUMN

Only the caudal vertebrae of the Solnhofen specimen can be compared. The general bauplan agrees very well with the Eich-

←

Figure 10. Wing skeleton of the Solnhofen specimen. **A.** Left and right wings in natural size. **B.** Detail of right manus showing the first and second phalanges of digit three underneath the first phalanx of digit two. The arrow points to the "articulation" separating the two proximal phalanges of digit three (3×). **C.** Claw of the second digit of the left manus showing the horny sheath (3×). **D.** Claw of the first digit of the right manus showing the horny sheath (3×).

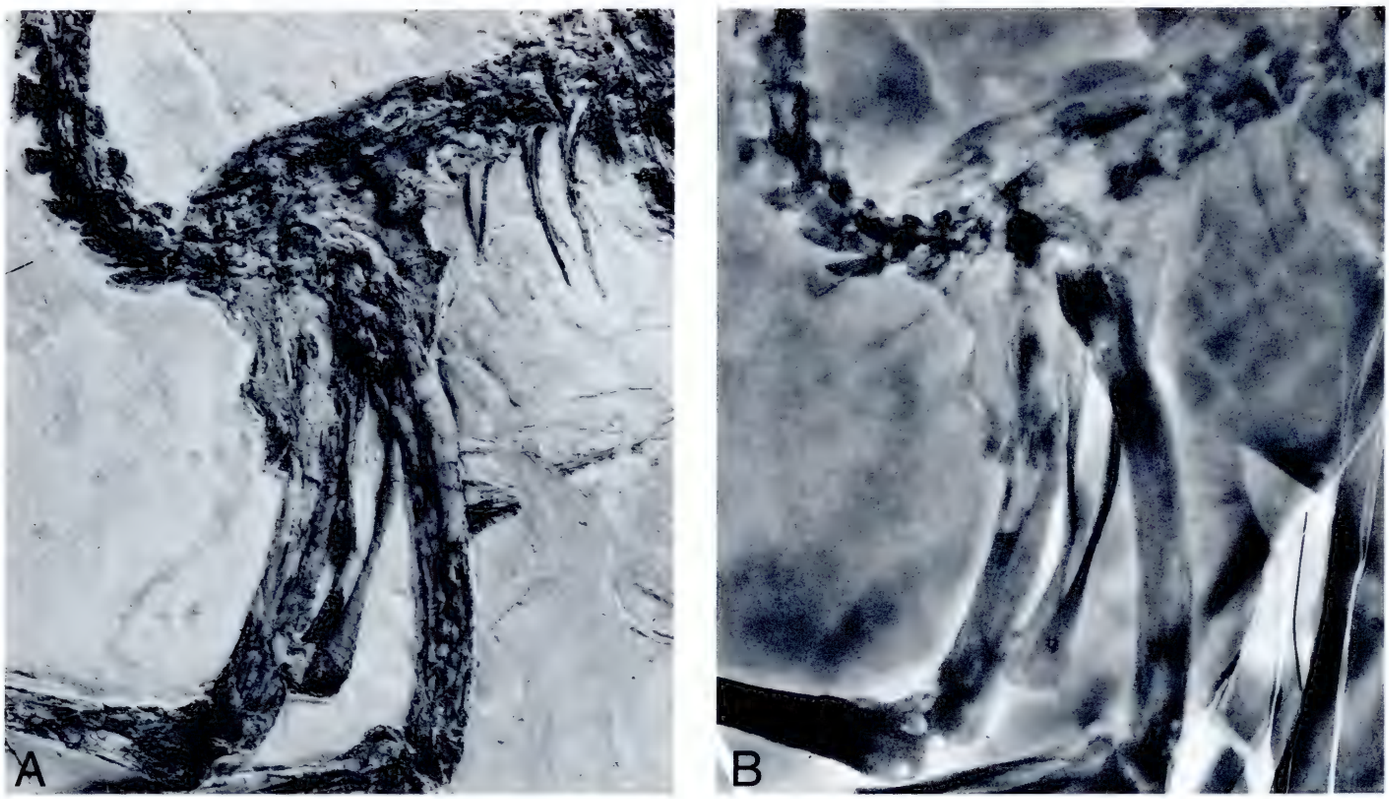

Figure 12. Pelvic region in the Solnhofen specimen; natural size. **A.** Photograph. **B.** X-ray photograph.

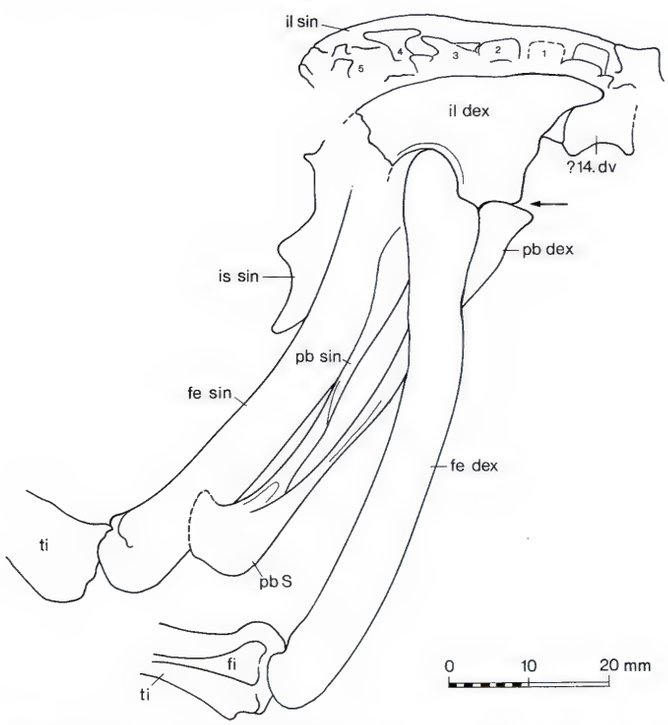

Figure 13. Pelvic region as preserved in the Solnhofen specimen. The arrow indicates the postmortem displacement of the right pubis at the pubic peduncle of the ilium. Abbreviations: **dv,** dorsal vertebra (?14th); **fe dex,** right femur; **fe sin,** left femur; **fi,** fibula; **il dex,** right ilium; **il sin,** left ilium; **is sin,** left ischium; **pb dex,** right pubis; **pb S,** pubic symphysis ("pubic foot"); **pb sin,** left pubis; **ti,** tibia.

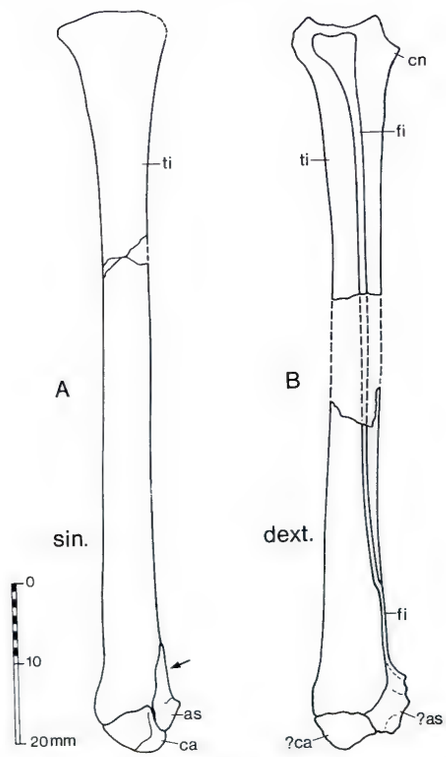

Figure 14. **A.** Left tibia in medial view. The arrow points to the ascending process of the astragalus. **B.** Right tibia and fibula in lateral view. Solnhofen specimen. Abbreviations: **as,** astragalus; **ca,** calcaneum; **cn,** internal cnemial crest; **fi,** fibula; **ti,** tibia.

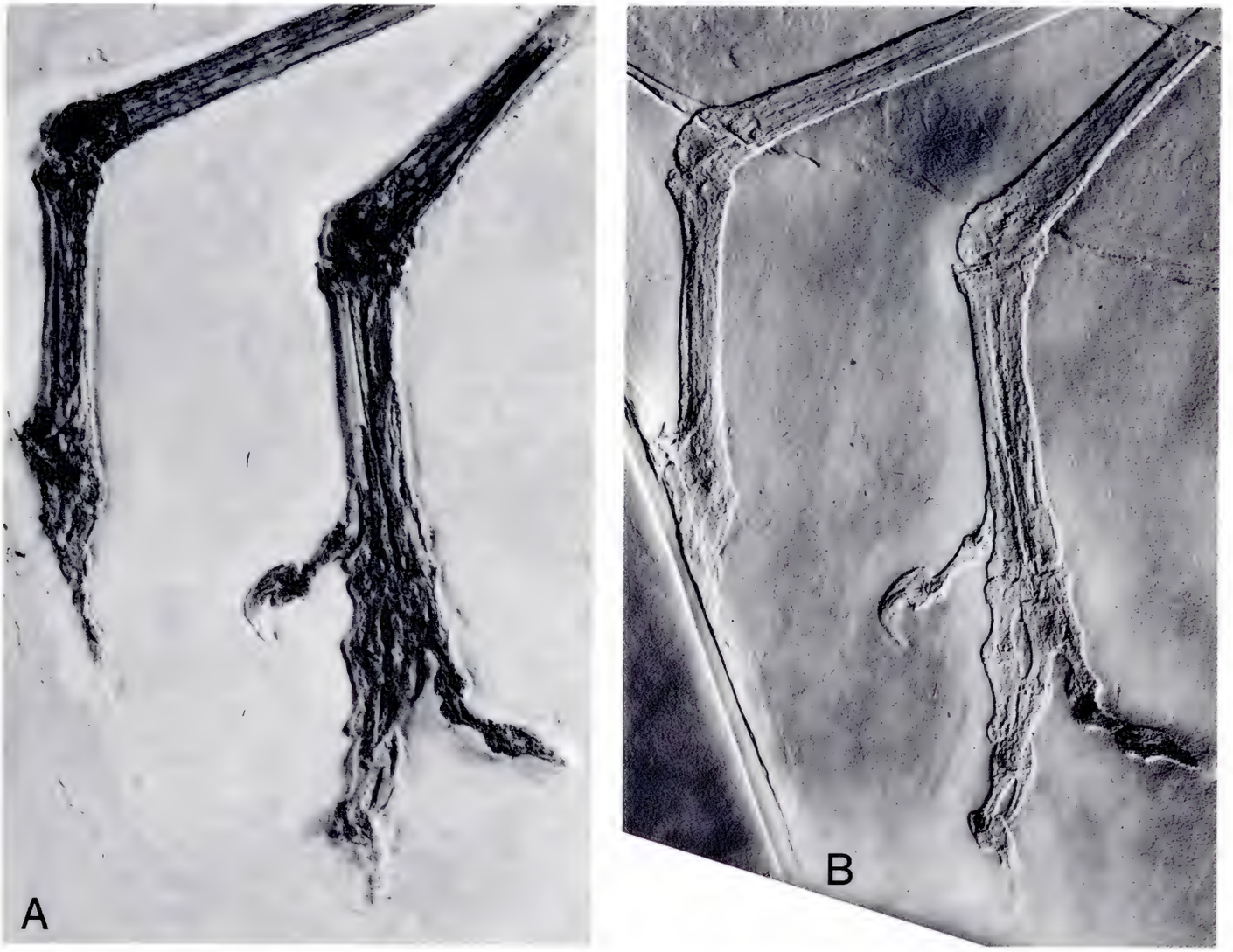

Figure 15. Left and right foot skeleton of the Solnhofen specimen; natural size. **A.** Photograph. **B.** X-ray photograph in relief technique.

stätt specimen, which has the best-preserved tail. This also includes the peculiar shape of the haemapophyses.

SHOULDER GIRDLE

The scapula and coracoid are apparently not as tightly fused as is observed in the London, Berlin, and Maxberg specimens (Ostrom, 1976b:116). With a narrow, strap-like shape and pronounced acromion process, the scapula is identical with that of the other specimens. Only the lateral surface of the coracoid is visible, and it is not directly comparable with the coracoid of the London specimen, where it is mainly the anterior side that is exposed.

WING SKELETON

The elements of the wing skeleton agree with those of the other specimens in every osteological detail as far as they are preserved, even to their position and relative proportions.

PELVIS

Neither the ilium nor the ischium are completely preserved. The typical shape of the posteroventral margin of the ischium is the same as in the Eichstätt specimen. The length of the pubes is proportionally similar, as in the other specimens. Distally, they were fused in a short symphysis, forming a hooklike "pubic foot," which has the same shape as in the Eichstätt and Berlin specimens. In the London specimen, the pubes are exposed in posterior view and reveal that the symphysis proper, the pubic foot, was also short, as is true for the Eichstätt specimen.

The orientation of the preserved pubes is different among all specimens. This is not surprising when one considers that in every individual skeleton of *Archaeopteryx* the contact of the pubes with the ilium and the ischium was apparently loose. The amount of postmortem displacement depended on sedimentological factors and the mode of compaction and compression of the skeletons.

HINDLIMBS

Osteological characters of the femur, tibia, and fibula are not distinct in the other specimens. The ratios of the humerus and femur range from 0.81 to 0.84 in the Solnhofen, London, Maxberg, and Berlin specimens. In the Eichstätt specimen, however, with a ratio of 0.89, the femur is relatively longer. The ratios of the femur and tibia range from 1.28 to 1.33 in the Solnhofen,

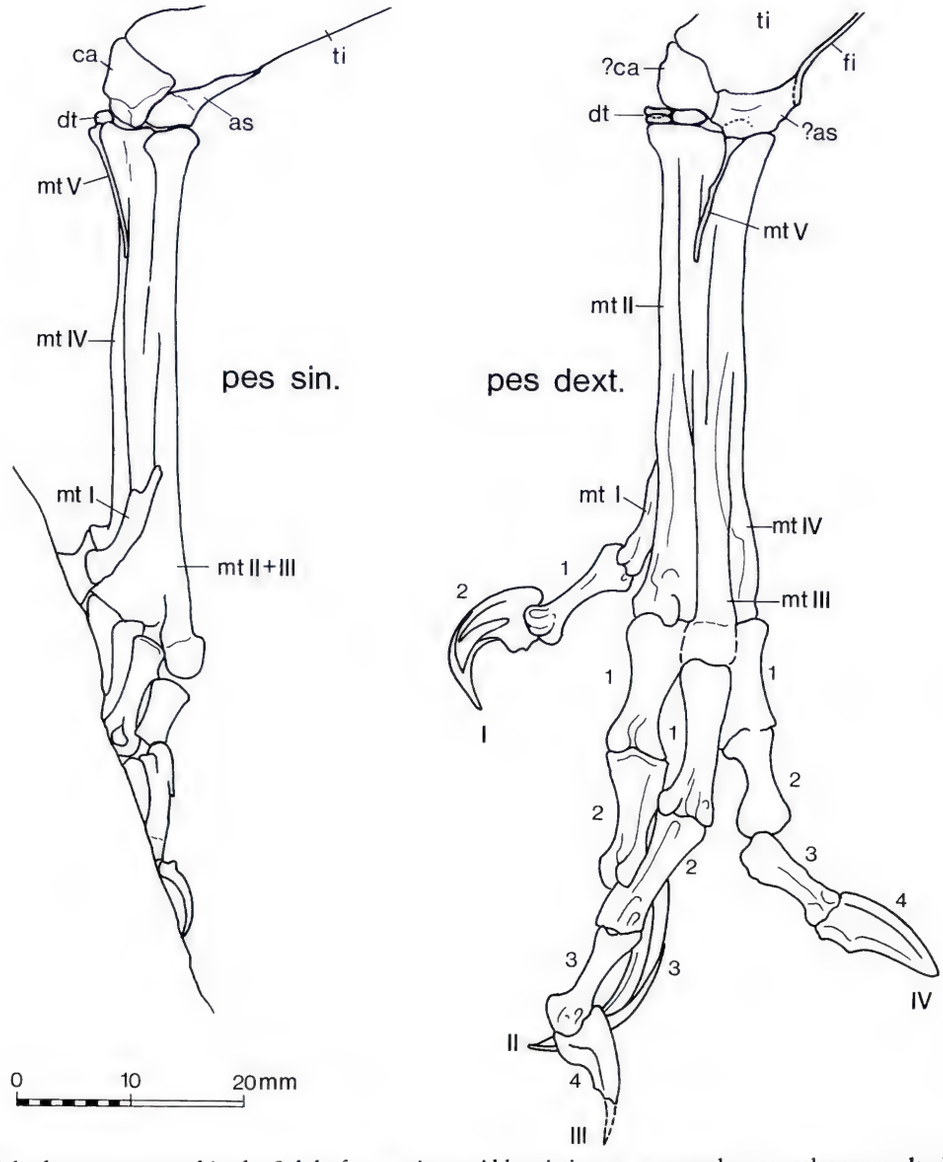

Figure 16. Left and right foot as preserved in the Solnhofen specimen. Abbreviations: **as,** astragalus; **ca,** calcaneum; **dt,** distal tarsals; **fi,** fibula; **mt I–V,** metatarsals I–V; **ti,** tibia.

London, and Berlin specimens, but it is 1.42 in the Eichstätt specimen. The ratios for the Maxberg and Haarlem specimens (1.38 and 1.48, respectively, in Table 3) are based on estimates and apparently are too high.

There is general agreement among the several specimens with respect to the tarsus and metatarsus. The astragalus, with an ascending process, is also found in the Eichstätt specimen. The three principal metatarsals of the Solnhofen specimen seem to be fused to a certain degree, which could be interpreted as an age indicator. The foot of the Solnhofen specimen is relatively short. It is relatively longer in the London and Berlin specimens. The longest feet, proportionally, are found in the Eichstätt individual. The most striking difference among the specimens is in the number of phalanges of the fourth toe. Only four are present in the Solnhofen specimen, whereas five are present in the Eichstätt and Berlin specimens, resulting in phalangeal formulas of 2–3–4–4–0 and 2–3–4–5–0, respectively. The situation in the London specimen is not clear (de Beer, 1954). No complete foot skeletons are preserved in the Maxberg and Haarlem specimens. This aberrant condition, i.e., only four phalanges of the fourth toe, which is shown in only one foot, is interpreted here as an anomaly.

In conclusion, the general conformity in so many osteological details and proportions with the specimens of London, Maxberg, Haarlem, and Berlin suggests that the Solnhofen specimen should be assigned to the same genus and species: *Archaeopteryx lithographica* von Meyer. The differences in size among these specimens are attributed to different ages, different sex, or both.

THE SYSTEMATIC POSITION OF THE EICHSTÄTT SPECIMEN

Mayr (1973), in his preliminary description of the Eichstätt specimen, suggested that this specimen should be assigned to a distinct, smaller species of *Archaeopteryx*. This author (Wellnhofer, 1974), however, regarded the specimen as a juvenile, not

yet fully grown individual of *Archaeopteryx lithographica*. He suggested as juvenile characters the following: (1) scapula and coracoid not yet fused, (2) metatarsals separated, and (3) furcula missing, probably not yet ossified. The relatively longer hindlimbs and tail of this specimen were interpreted to be a result of positive allometric growth.

Howgate (1984c) separated the Eichstätt specimen as a distinct species, *Archaeopteryx recurva*, and gave the following diagnosis: (1) teeth more gracile and recurved, (2) specimen is one-third smaller than the other specimens, (3) distal elements of the pes are proportionally longer, and (4) pubic symphysis is short.

Later, Howgate (1985) was convinced that the Eichstätt specimen must also be separated generically, as *Jurapteryx*, mainly because (1) the pubis was very slightly opisthopubic or vertical, (2) an ossified furcula was absent, and (3) the metatarsals were unfused.

In evaluating the taxonomy of the Eichstätt specimen, those characters that could be interpreted in different ways, i.e., as a result of sexual dimorphism, or ontogeny, must not be taken into account. One of these features is individual size, because it could depend on age, or sex, or both. If size were to be used as a diagnostic species character, at least five individuals of *Archaeopteryx* could be assigned to different species. Equally, the relatively longer hindlimbs and feet of the Eichstätt specimen could be explained as a species character or as a sexual feature, or as an indication of positive allometric growth of a larger species.

Moreover, whether *Archaeopteryx* had a reptilian or an avian growth pattern is not known. The epiphyseal sutures seen in juvenile birds are not known in any of the *Archaeopteryx* specimens. But this is only negative evidence. The fact that all known individuals of *Archaeopteryx* are of different sizes, although osteologically uniform, rather suggests a reptilian growth pattern of almost permanent, although decreasing, growth. If this is the case, then the hindlimbs and tail of *Archaeopteryx* have a positive growth allometry. This is reasonable if we presume that the running ability of a young individual was of vital importance, particularly before full flight capability was achieved.

The degree of ossification in the skeleton is unequivocally growth-dependent. The long bones of the Eichstätt specimen all appear to be well ossified, but the fusion of certain elements should also be considered. The Eichstätt specimen has clearly separated metatarsals, whereas in the Maxberg specimen Heller (1959) could show a proximal fusion of the metatarsus. Also, in the new Solnhofen specimen, the three principal metatarsals are partially fused. This tendency toward fusion of the metatarsals of *Archaeopteryx* can be evaluated in light of the evolution toward the single tarsometatarsus seen in modern birds.

The fusion of the scapula and coracoid apparent in the London specimen is not developed in either the Eichstätt or the new Solnhofen specimen. This character obviously cannot be used in an ontogenetic interpretation. These two bones do not fuse in modern birds either.

Although new X-ray photographs of the Eichstätt specimen were taken, using a new processing technique, a furcula could not be found. Three explanations are possible: (1) the skeleton was lacking a furcula, as suggested by Howgate (1985), (2) the furcula was present, but was lost because of postmortem processes before or after the deposition of the bird's body, or (3) the furcula was present, but still membranous, not yet ossified and, thus, not fossilized.

In my opinion, the first possibility is the least probable one. The detailed osteological similarities between the Eichstätt specimen and the other specimens are so striking that it would be very strange if only this element failed to have been developed. It is more likely that the furcula was present and was lost postmortem because the connection of this bone with the shoulder girdle was relatively loose. The furcula could also have been removed along with a piece of the main slab that is missing from this area. On the other hand, no other bone of the fully articulated Eichstätt skeleton is missing, which means that it was imbedded in the sediment with its soft parts still intact. Was the furcula not preserved because it was not yet ossified? If so, one must assume that only this element, of the entire skeleton, was ossified at a rather late stage in the ontogeny.

In establishing a new species of *Archaeopteryx*, Howgate (1984c) pointed out that the pubic symphysis in the Eichstätt

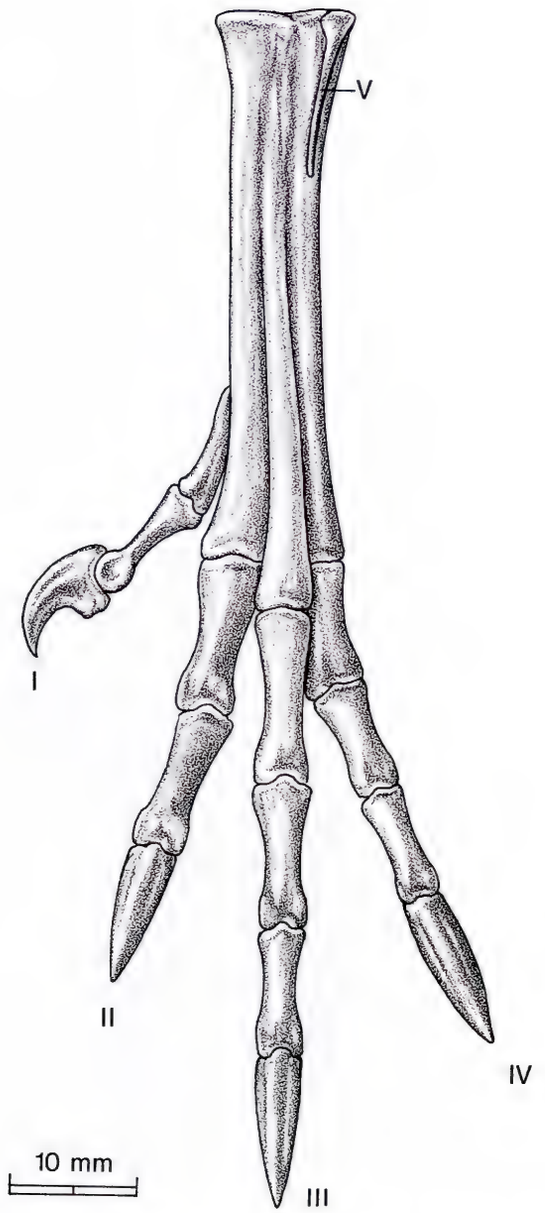

Figure 17. Restoration of the right foot of the Solnhofen specimen, in dorsal view. Note the four phalanges of the fourth toe instead of five.

Figure 18. Detail of the Solnhofen specimen in low-angle illumination showing the feather shaft impressions of the left wing as distinct furrows; natural size.

specimen was short, whereas it was long in the other specimens, and he takes this as a diagnostic character. However, in the new Solnhofen specimen, as well as in the London specimen, the co-ossified part of the symphysis, the pubic foot, is also short. The apron-like medial extensions of the pubic shafts, as shown in the London specimen, are only in medial contact but not fused (Wellnhofer, 1985).

As was pointed out earlier, all specimens of *Archaeopteryx* with preserved pelves (Solnhofen, London, Maxberg, Berlin, and Eichstätt) show that the pubes had only loose contacts with the ilia and ischia. Consequently, they are all more or less displaced and do not reveal their original orientation. On the other hand, it is possible to restore the pubes of all specimens to a relatively uniform orientation of between 110° and 130° relative to the sacral line (Wellnhofer, 1985). No evidence indicates that the pubes in the Eichstätt specimen were oriented at a steeper angle than in the other specimens.

The last character on which Howgate (1984c, 1984d) based

Table 1. Measurements (mm) of the Solnhofen specimen of *Archaeopteryx lithographica*. *, approximate measurements; +, bone incomplete.

Skull	
Length, restored	65*
Naris length	12
Mandible length, restored	61*
Vertebral column	
(?)3rd cervical	9*
(?)12th dorsal	8*
(?)13th dorsal	8*
(?)14th dorsal	8.8
Sacrum length, restored	28*
Tail length, restored	240*
1st caudal	5.4
2nd caudal	6.2
3rd caudal	6.7
4th caudal	6.5
5th caudal	7.5
6th caudal	9.0
7th caudal	9.7
8th caudal	9.5
9th caudal	13.0
10th caudal	14.2
11th caudal	14.3
12th caudal	15.5
13th caudal	15.0
14th caudal	11*
15th caudal	11*
16th–23rd caudal	80*
Scapula length, preserved	41
Scapula length, restored	51*
Scapula, medial width	4
Scapula, proximal width	10
Coracoid length	24.5
Coracoid, proximal width	8
Wing skeleton, total length	260*
Humerus length	83.0
Humerus, middle width of shaft	6.8
Humerus, proximal width	15.0
Humerus, distal width	11.0
Ulna length, restored	72*
Ulna, medial width	4.5
Ulna, proximal width	7.5
Radius length, restored	69*
Radius, medial width of shaft	3.5
Radius, proximal width	5.5
Metacarpal I	7.5+
Metacarpal II	34.3+
Metacarpal III	33.1+
Digit I of manus length	45.9
1st phalanx, left	28.0
1st phalanx, right	28.4
2nd phalanx, ungual	17.5
Digit II of manus length	65.4
1st phalanx	20.1
2nd phalanx	27.5
3rd phalanx, ungual	17.8
Digit III of manus length	43.6
1st phalanx	8.0
2nd phalanx	6.5
3rd phalanx	17.8
4th phalanx, ungual	12.0
Total length of manus	105*
Ilium length, restored	38*
Ischium length, restored	24.5*
Pubis length	59.3
Acetabulum diameter	7.5*
Hindlimb, total length	255*
Femur length	70*
Femur, medial width of shaft	6.5
Femur, diameter of caput	5.5
Femur, distal width	9.0
Tibia length	89.5
Tibia, medial width	6.0
Tibia, proximal width	12*
Tibia, distal width	10*
Fibula length	82.4
Fibula, medial width	0.6
Fibula, proximal width	3.0
Metatarsal I	10.0
Metatarsal II	43.5
Metatarsal III	47.8
Metatarsal IV	44.5
Metatarsal V	10.5
Digit I	
1st phalanx	10
2nd phalanx, ungual	10.5
Digit II	
1st phalanx	12.0
2nd phalanx	12.5
3rd phalanx, ungual	14*
Digit III	
1st phalanx	14
2nd phalanx	13
3rd phalanx	10.5
4th phalanx, ungual	10*
Digit IV	
1st phalanx	10
2nd phalanx	8.5
3rd phalanx	9.0
4th phalanx, ungual	11+
Foot length	95*

his conclusions was the different dentition of the Eichstätt specimen. It seems natural that the teeth of the smallest individual would be relatively more gracile than those of the larger ones. In arrangement and morphology, however, the premaxillary and maxillary teeth agree very well with those of the Berlin specimen. This includes not only the tooth formula (4 premaxillary/8 maxillary teeth) but also the peculiar constriction of the crowns of the second, third, and fourth premaxillary teeth. Only the tips of the fourth premaxillary and the third maxillary teeth are recurved, and equally so in both specimens.

Bühler (1986) has pointed to the fact that much greater differences in the teeth of juvenile and adult individuals of modern crocodiles and monitor lizards are known than those seen in the several specimens of *Archaeopteryx*.

With consideration of all these aspects, and after the study of the new Solnhofen specimen, I come to the same conclusion as before (Wellnhofer, 1974) and determine that the Eichstätt specimen is an immature individual of the same species and

Table 2. Measurements (mm) of skeletal elements in the specimens of *Archaeopteryx*. *, approximate measurements.

	Solnhofen	London	Maxberg	Haarlem	Berlin	Eichstätt
Skull	65*	—	—	—	52*	39*
Humerus	83.0	75	72	—	63.5	41.5
Ulna	72*	67.5	62 (?)	—	55	36.5
Manus (mc II + digits)	105*	—	—	—	77	52.8
Wing skeleton	260*	—	—	—	195.5	130.8
Femur	70*	60.5	58*	54*	52.6	37.0
Tibia	89.5	80.5	80 (?)	80 (?)	68.5	52.5
Pes (mt II + digits)	95*	89	—	—	75*	61.7
Hindlimb	254.5*	230	—	—	196*	151.2

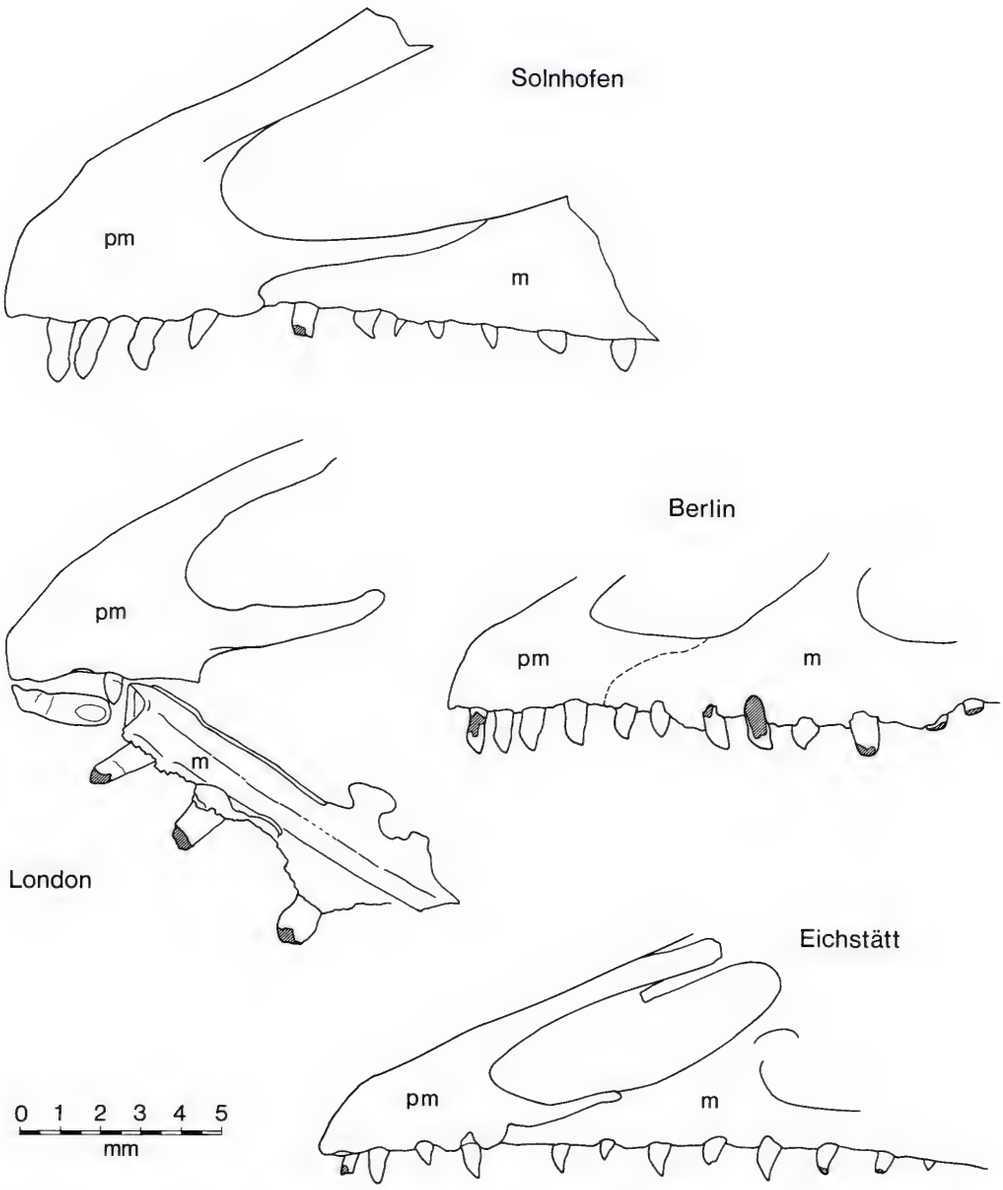

Figure 19. Comparative drawings of the upper jaws showing the dentitions of the Solnhofen, London, Berlin, and Eichstätt specimens, drawn to the same scale. The Solnhofen and Eichstätt specimens are original drawings; the London and Berlin specimens are redrawn after Howgate (1984c). Abbreviations: **m,** maxilla; **pm,** premaxilla.

Table 3. Ratios of skeletal elements of the six *Archaeopteryx* specimens according to the measurements given in Table 2, on the basis of the Solnhofen specimen.

	Solnhofen	London	Maxberg	Haarlem	Berlin	Eichstätt
Humerus	1	0.90	0.87	—	0.77	0.50
Ulna	1	0.94	0.86	—	0.76	0.51
Manus	1	—	—	—	0.73	0.50
Wing skeleton	1	—	—	—	0.75	0.50
Femur	1	0.86	0.83	0.77	0.75	0.53
Tibia	1	0.90	0.89	0.89	0.77	0.59
Pes	1	0.94	—	—	0.79	0.65
Hindlimb	1	0.90	—	—	0.77	0.59
Humerus : manus : ulna	1:0.87:1.27	1:0.90:—	1:0.86:—	—	1:0.87:1.40	1:0.88:1.27
Femur : tibia : pes	1:1.28:1.36	1:1.33:1.47	1:1.38:—	1:1.48:—	1:1.30:1.43	1:1.42:1.67
Humerus : hindlimb	1:3.07	1:3.07	—	—	1:3.09	1:3.64
Humerus : femur	1:0.84	1:0.81	1:0.81	—	1:0.83	1:0.89
Humerus : tibia	1:1.08	1:1.07	1:1.11	—	1:1.08	1:1.27
Humerus : pes	1:1.14	1:1.19	—	—	1:1.18	1:1.49
Wing skeleton : hindlimb	1:0.98	—	—	—	1:1.0	1:1.16

genus as the other specimens, namely *Archaeopteryx lithographica* (see also Houck et al., 1990).

Of course, it cannot definitely be excluded that the Eichstätt specimen is a distinct species. But one is forced to think not only about the systematic position of the Berlin specimen, but also that of the other specimens. Recently, Stephan (1987) has listed all the differences between the individual specimens suggested by previous authors. Consequently, he splits the five specimens into three different genera and species: *Archaeopteryx macrura* Owen (for the London, Maxberg, and Haarlem specimens), *Archaeornis siemensi* (Dames) (for the Berlin specimen), and *Jurapteryx recurva* (Howgate) (for the Eichstätt specimen).

In this scheme, the taxon *Archaeopteryx lithographica* is considered uncertain because it was not totally clear whether von Meyer (1861) wanted to apply this name to the isolated feather or to the skeleton, which later became the London specimen.

As long as nothing is known about the variability and possible sexual dimorphism of *Archaeopteryx*, I do not think that the naming of so many species is of much help. With regard to the establishment of a different genus for the Eichstätt specimen, I agree with Bühler (1986), who reasoned that a generic separation would only be justifiable if a diphyletic or polyphyletic origin could be demonstrated. This, however, is not the case.

SUMMARY

A new specimen of *Archaeopteryx* from the Upper Jurassic Solnhofen limestone of Bavaria was discovered in a private fossil collection in Solnhofen in 1987. It is the sixth skeletal specimen and the largest individual of *Archaeopteryx* known. Based on the total length of the wing skeleton, the differences in size are 10 percent to the London specimen, 13 percent to the Maxberg and Haarlem specimens, 25 percent to the Berlin specimen, and 50 percent to the Eichstätt specimen. The fairly complete skeleton is preserved in its natural articulation; however, bone material was lost when the slab was broken during or after excavation, including parts of the skull, some vertebrae, both carpal regions, and most of the digits of the left foot. The front end of the snout and the mandible with most of the dentition are preserved. The premaxillary teeth show a slight constriction halfway up the crowns, which is very similar to the London and Berlin specimens. The distal section of the tail must have been rather rigid as a result of the development of elongated, rod-like extensions of the haemapophyses and zygapophyses.

There is no ossified sternum, but a fragment of the furcula is present. The scapula and coracoid are not fused in the new specimen, which is in contrast to the condition seen in the London specimen. All claws of the digits retain their horny sheaths. They are strongly curved and have very sharp tips. The third digit of the manus has four distinct phalanges and typically crosses the second finger.

Both pubes are fused in a ventral symphysis that forms a hook-like "pubic foot," as documented in the London, Berlin, and Eichstätt specimens. A nearly vertical orientation of the pubes is indicated. The astragalus has an ascending process, which is theropod-like. The principal metatarsals show signs of fusion, which is interpreted to be an age indicator. The phalangeal formula of the pes appears to be different from the normal count because there are only four phalanges in the fourth toe instead of five. This condition seems to be an anomaly in this individual. Impressions of the shafts of the left wing feathers indicate once again that *Archaeopteryx* had feathers.

Comparisons of the new specimen with the other specimens of *Archaeopteryx* reveal close similarities with regard to osteological characters, as well as to the proportions of skeletal elements. This is especially the case with the London specimen, but there is also a general conformity of the osteological details and proportions with the specimens of Maxberg, Haarlem, and Berlin. This suggests that the new specimen should be assigned to *Archaeopteryx lithographica* von Meyer. The differences in size are attributed to differences in age, sex, or both.

Although osteologically very similar, the Eichstätt specimen is half the size of the new specimen, and it differs also from the other individuals in having relatively longer hindlimbs. The lack of an ossified furcula and the still separated, unfused metatarsals point to the immaturity of the Eichstätt individual. It is considered to be a half-grown *Archaeopteryx lithographica* and not a distinct taxon as proposed by Howgate (1984c). If this is correct, the hindlimbs of *Archaeopteryx* have a positive growth allometry with a reptilian rather than an avian growth pattern.

The new specimen of *Archaeopteryx* is housed in the "Bürgermeister Müller Museum" of the community of Solnhofen and, thus, is introduced here as the "Solnhofen specimen" of *Archaeopteryx*.

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COMMENTS ON THE NEW (SOLNHOFEN) SPECIMEN OF *ARCHAEOPTERYX*

John H. Ostrom

ABSTRACT. Recognition of a sixth skeletal specimen of *Archaeopteryx* further documents key anatomical conditions preserved in the other specimens, especially the configuration of the manus, but fails to establish the correct manus digital identity. The new specimen does, however, preserve an unexpected construction of the pes.

Key words: *Archaeopteryx*, manus, pes, feathers.

Announcement of the discovery of another specimen of *Archaeopteryx* von Meyer 1861 (Wellnhofer, 1988) raises a number of questions that have not been entirely answered by the previously known specimens. First and most important is the issue of its taxonomic assignment. Is this new specimen truly assignable to *Archaeopteryx*, and, if so, specifically to *Archaeopteryx lithographica* von Meyer 1861? Six skeletal specimens are now known and referred to *Archaeopteryx*, of which this latest specimen, the largest, is twice the size of the smallest example—the Eichstätt specimen. Howgate (1985) has proposed to assign the Eichstätt specimen to a separate genus and species—*Jurapteryx recurva*. We all recall that the Berlin specimen was assigned early on to a distinct taxon *Archaeopteryx siemensi* (Dames 1887) and later assigned to a distinct genus *Archaeonis* (Petronievics 1921), but current opinion places it in *Archaeopteryx lithographica*. Clearly, there are reasons to suspect that the six specimens now known represent more than one species—and perhaps more than one genus. But how do we determine this with such a small sample? I think the current practice of individual specimen designation, e.g., London, Berlin, Maxberg, etc., is preferable to the formal naming of separate species. This may be ducking the issue, but I just do not think that we have enough information to justify anything else at the moment.

On anatomical matters there are many questions, but I will address only a few that are illuminated by the new specimen. The configuration of the manus in *Archaeopteryx* has been a matter of diverse interpretation and disagreement in recent years. Most important is the controversy over which fingers (digits) are present in the manus of living birds and which are represented in *Archaeopteryx*. Are they I, II, and III? Or are they II, III, and IV? The new specimen does not and cannot answer that question. Paleontologists have traditionally labeled the digits in *Archaeopteryx* (Fig. 1) as the first three digits (I, II, and III), but developmental biologists, e.g., Hinchliffe (1985), argue on the

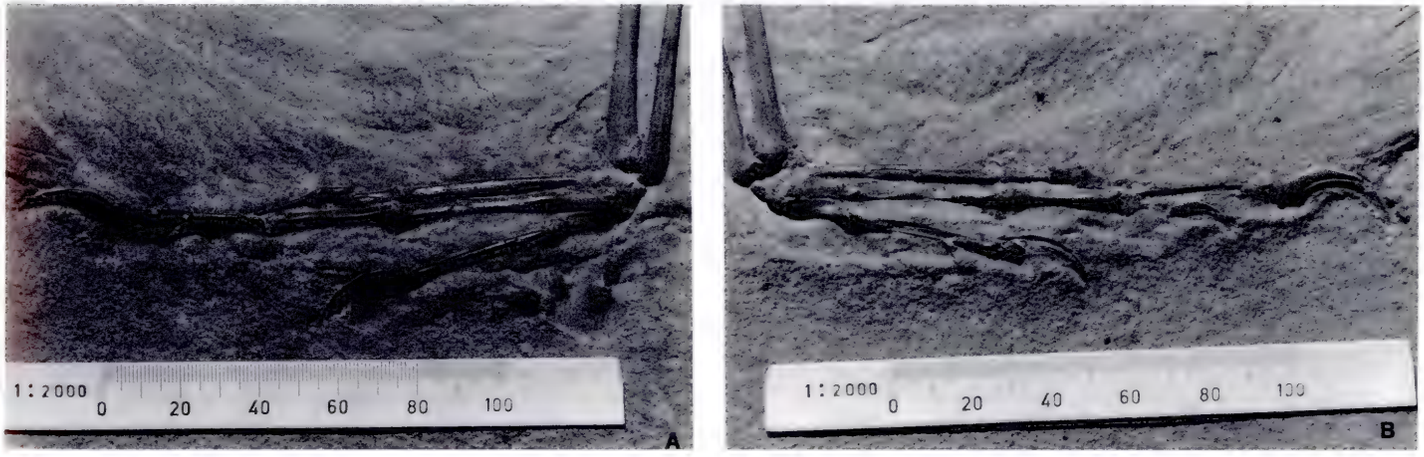

Figure 1. The right (**A**) and left (**B**) manus of the Berlin specimen of *Archaeopteryx*. The phalangeal formula of the three remaining digits either preserves or "mimics" the expected primitive formula of the first three digits. These photographs also illustrate the crossed digits.

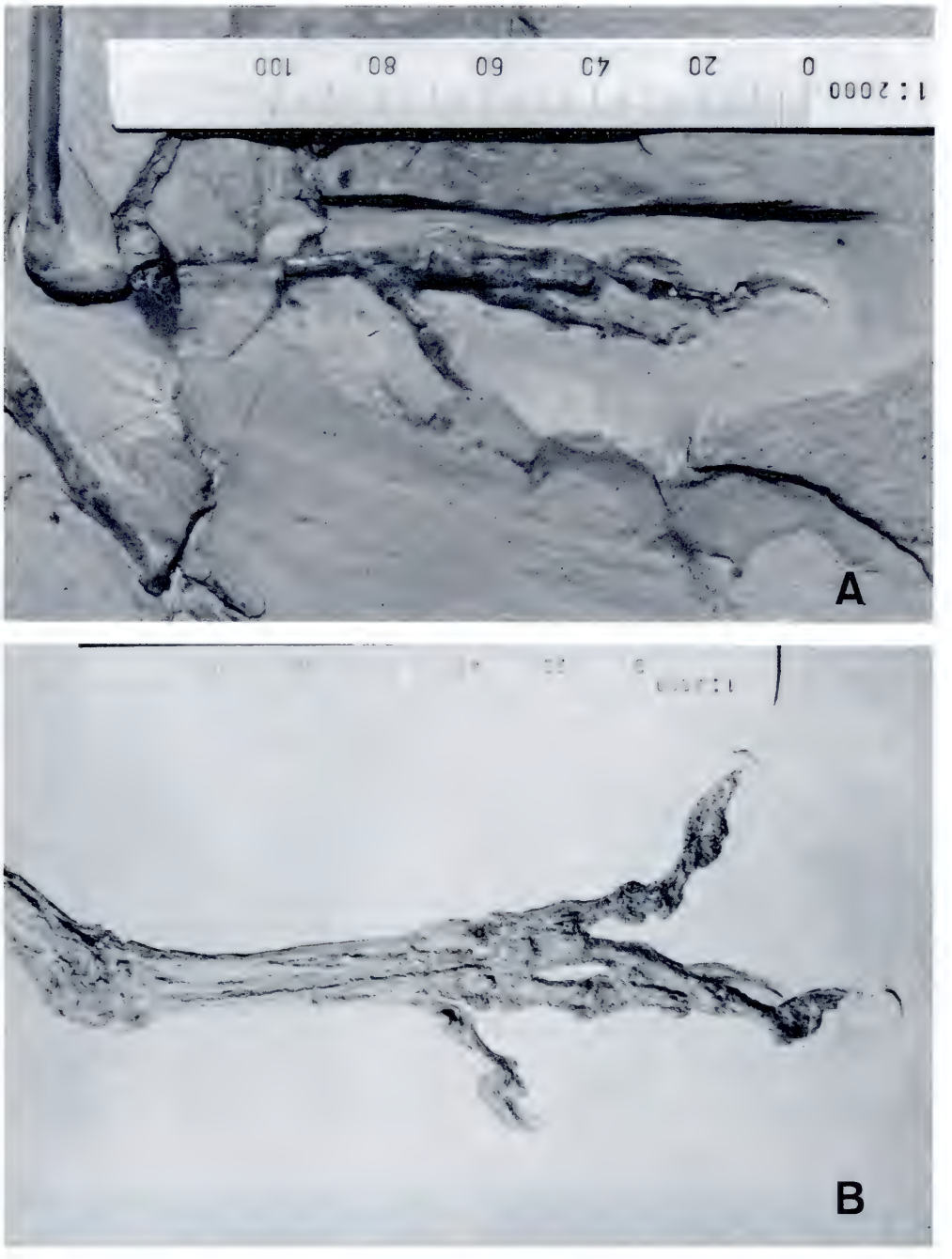

Figure 2. The left foot (**A**) of the Berlin specimen compared with the right foot (**B**) of the new Solnhofen specimen of *Archaeopteryx*.

basis of embryologic evidence that avian wing digits are actually the three middle fingers. Without any embryologic evidence from *Archaeopteryx* we simply cannot say—either about *Archaeopteryx or* about modern birds.

Critics to the contrary, this question of digital identity *is* a crucial matter in the whole issue of whether *Archaeopteryx* was on the main line of descent leading to modern birds, or merely a side branch in early avian evolution. Despite the fact that this cannot ever be answered on embryologic grounds, for obvious reasons, it is important because the embryologic evidence presented by Hinchliffe (1985) is the *only* evidence offered so far that *possibly* precludes a direct ancestral position of *Archaeopteryx* in the phylogeny leading to modern birds. No other contradictory evidence has been cited.

Yet, the new specimen does provide some information that is relevant to this question. The labels that have been applied to the digits in *Archaeopteryx* have been based on its preserved phalangeal formula of 2–3–4, which theoretically is the primitive formula of the first three digits of the pentameral manus. To have acquired a 2–3–4 phalangeal formula with the three middle digits, *Archaeopteryx* must have lost digits I and V as well as one—and only one—phalanx from each remaining digit (II, III, and IV). In doing so, they would mimic the first three primitive digits. That seems most unlikely. None of the presently known

specimens of *Archaeopteryx* support the middle three digit hypothesis, or any other hypothesis for that matter, so the issue is not yet resolved.

However, the new specimen *does* show that the primitive phalangeal formula for the "first three" digits is in fact preserved in *Archaeopteryx*. The Solnhofen specimen clearly preserves a distinct joint in the outer finger, and the true phalangeal formula of the manus is 2–3–4. This is proof that the strange interpretation of Tarsitano and Hecht (1980) of a "broken phalanx" in the outer digit in several specimens of *Archaeopteryx* (leaving a presumed manual formula of 2–3–3) is incorrect. However, that determination does not conclusively resolve the question of which fingers are present in *Archaeopteryx*, or in modern birds.

There is another curious bit of information preserved in the new specimen that has yet to be explained: the fact that the two longest digits, the outer digits, are crossed. That same condition is preserved in the Berlin specimen, in the Maxberg specimen, *and* in the Eichstätt specimen. Why? I cross my fingers on occasion, but I doubt if *Archaeopteryx* had similar motivation. It has been suggested that these crossed digits might have provided a more rigid platform for attachment of the primary flight feathers. Or, perhaps it was the first stage of fusion of the avian digits.

So much for the manus. Let me now turn to the foot. Here we have a completely different state of affairs. The Berlin and Eichstätt specimens clearly preserve the expected primitive phalangeal formula for the remaining four toes I, II, III, and IV, which is 2–3–4–5. BUT, the new specimen shows a different phalangeal formula of 2–3–4–4! (Fig. 2). Unfortunately, only the right foot is intact in the new specimen, so absolute verification of this formula is not possible. It must be noted, however, that de Beer (1954) suspected that the foot phalangeal formula in the London specimen was 2–3–4–4. The actual condition remains in doubt because the fourth toe of the London specimen is obscured by the third toe, and until X-ray or CAT scans are performed on the specimen we will not know. The important fact, though, is that the new specimen possesses an unexpected foot construction. Thus, the critical question is: Is this distinction sufficiently different from the other specimens to justify designation of the Solnhofen specimen as a separate species or genus? I think not, and here is why.

In a recent paper (Alberch and Gale, 1985), developmental anomalies of digital reductions in amphibians were reviewed. The conclusion was that, at least in amphibians, most of the diversity in digital morphology can be explained as reflections of developmental patterns and sequences. Interruptions of normal developmental processes result in different morphologies within a single species. Their analysis, and similar studies (e.g., Goodwin and Trainer, 1983; Newman and Frisch, 1979; Oster and Alberch, 1982; Stock and Bryant, 1981; Tickle et al., 1975) seem to argue that unusual phalangeal formulae or digital configurations, in and of themselves, are *not* sound bases for taxonomic distinction.

Finally, I have to make a public statement in ridicule of the outrageous claim by Hoyle and Wickramasinghe (1986) that the feather impressions in the London and Berlin specimens of *Archaeopteryx* are fake. They are not. Charig et al. (1986) demonstrated the absurdity of the Hoyle claim, yet it persists, especially among the uninformed creationist camps who cannot tolerate the hard evidence that *Archaeopteryx* provides to evolutionary theory. The new Solnhofen specimen, unknown before 1987, preserves clear impressions of feather shafts—further proof of the falsity of Hoyle's claim and documentation of the avian identification of the new specimen. The common expression "according to Hoyle" has no merit whatsoever.

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A COMPARATIVE STUDY ON THE CLAWS OF *ARCHAEOPTERYX*

Dieter Stefan Peters and
Ernst Görgner

ABSTRACT. In discussions about the origin of birds and their flight ability, the claws of *Archaeopteryx* have been regarded as indicative of a trunk-climbing function and, thus, as the main support for the arboreal hypothesis. The claws of trunk-climbing birds do indeed have a peculiar construction, but this also occurs in cliff climbers and in some species that do not climb at all (e.g., many cuckoos). Thus, the claws of *Archaeopteryx*, which in some regards are similar to the claws of climbers, are not necessarily indicative of a climbing function, all the more as they are very gracile, not at all or only poorly keratinized in their proximal third, and without signs of distal wear. The apparent contradiction between the claws, which have seemed to some as indicative of climbing, and all the other morphological features of *Archaeopteryx*, which are inconsistent with climbing habits (Peters, 1984), is thus eliminated. Hence, the weakened argument for an arboreal origin of flight provides indirect support for the hypothesis that the flight of birds began as a form of "ridge gliding."

ZUSAMMENFASSUNG. In der kontrovers geführten Diskussion über die Entstehung der Vögel und ihrer Flugfähigkeit spielen die Krallen von *Archaeopteryx* eine große Rolle. Nach Yalden (1985) sollen sie nur als Anpassung an das Stammklettern zu erklären sein. Unsere Untersuchungen zeigen, daß stammkletternden Vögeln tatsächlich ein bestimmter Bau der Krallen eigen ist, doch kommen solche Krallen bei Felskletterern und sogar bei manchen Vögeln, die nach unserer Kenntnis gar nicht klettern (z.B. viele Kuckucke), ebenfalls vor. Solche Krallen sind also kein untrüglicher Beweis für eine kletternde Lebensweise. Trotz ihrer Ähnlichkeit mit Kletterkrallen zeigen die Krallen von *Archaeopteryx* einige Besonderheiten, die ihre Kletterfunktion noch unwahrscheinlicher machen, nämlich ihre sehr zarte Beschaffenheit und das Fehlen von Abnutzungserscheinungen, wie sie viele Stammkletterer aufweisen. Die wirkliche Funktion der Flügelkrallen bleibt zwar weiterhin unbekannt, aber der Widerspruch zwischen den zahlreichen konstruktionsmorphologischen Befunden, die gegen eine arboricole Lebensweise der Urvögel sprechen (Peters, 1984) und den angeblich auf das Klettern hinweisenden Krallen, ist beseitigt. Die Vorstellung, daß der Vogelflug als "Hanggleiten" begann, gewinnt damit an Sicherheit.

Key words: *Archaeopteryx*, claws, flight.

INTRODUCTION

Although *Archaeopteryx* von Meyer 1861 has been known for nearly 130 years and is among the most famous of all fossils, the functional interpretation of its morphology is still at issue. Because *Archaeopteryx* obviously represents a transitional grade between reptiles and birds, the correct understanding of its properties may be essential for our idea of the early evolution of birds and the origin of flight.

In the course of the long-standing controversy about the beginning of flight, the claws of *Archaeopteryx* have been played as the arboreal theory's trump card. Yalden (1985) maintained that the construction of the claws of the manus was best explained as indicating a climbing function. This opinion was accepted by several authors (Bock, 1986; Bühler, 1986) in favor of the hypothesis that the prebird or protobird, whatever it might have been systematically, was a trunk-climbing creature. This presented a puzzling situation because all findings of the functional morphology of birds and *Archaeopteryx*, particularly those concerning the locomotory apparatus, e.g., orientation of bones and articulations in the forelimbs, bipedalism, and well-developed primaries (Sy, 1936; Stegmann, 1937; Martin, 1985; Ostrom, 1976, 1985; Gauthier and Padian, 1985; Peters, 1984, 1985), are inconsistent with this hypothesis. The claws appeared to be the only sound support for the arboreal theory. The contradiction of the arguments was intriguing enough to warrant further analysis of the claws of *Archaeopteryx* and some modern birds.

PRELIMINARY THEORETICAL CONSIDERATIONS

The function of an organismic structure is limited by its construction. This limitation is rather wide because organisms are active and greatly autonomous entities that can bring their structures into action in very different situations. Thus, as a rule it is easier to recognize what a structure could not be used for under any circumstances than to conclude its actual function from its construction.

Knowing the basic anatomy of a claw we can predict what a claw used for trunk climbing should look like. To obtain a hold on tree bark, it should be sharply pointed; to avoid the energy demanding flexion of the fingers or toes, it should have a strong, but not too strong, curvature; being stressed mainly vertically along its longitudinal axis, its cross section should be broad dorsoventrally but narrow lateromedially. A claw built like this would in all probability make a good climbing hook. However, there are no inherent natural laws warranting that every pointed, strongly curved, and narrow claw must be inevitably a claw used for trunk climbing. From this we can deduce the hypothesis

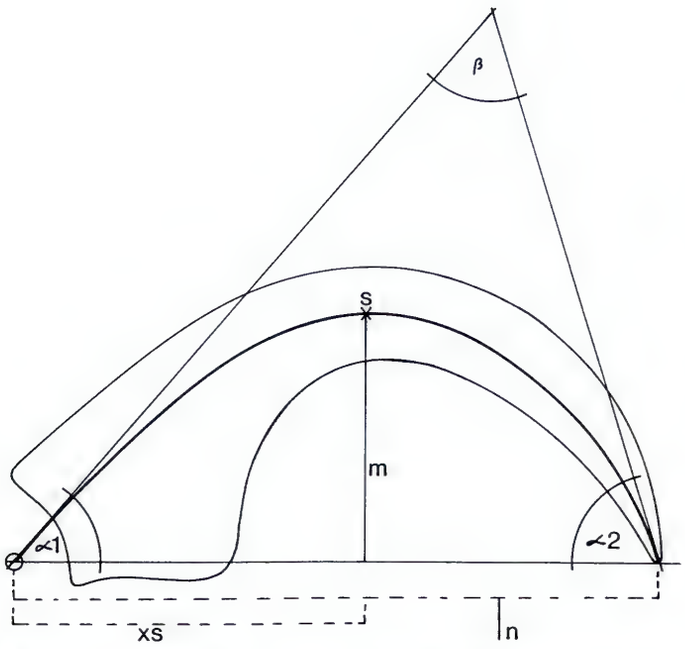

Figure 1. Measuring the curvature of a claw. Because the dorsal and ventral curvatures are different, a mean (or ideal) curvature is measured. This is a curved line defined by three points: the fulcrum (open circle), tip of the claw, and S, which is located perpendicularly below the vertex of the dorsal curvature and halfway between the dorsal and the ventral edge. *m* is perpendicular to *n* (the straight line between the fulcrum and the point of the claw). (For further explanation, see text.)

that narrow, curved, and sharply pointed claws are not confined to trunk climbers. Herein we test this hypothesis.

MATERIAL AND METHODS

The claws of the following species were measured: *Archaeopteryx;* Accipitridae: *Accipiter gentilis* Linnaeus 1758, *Buteo buteo* Linnaeus 1758; Falconidae: *Falco tinnunculus* Linnaeus 1758; Phasianidae: *Gallus gallus* Linnaeus 1758; Psittacidae: *Lorius roratus* (P.L.S. Müller 1776); Cuculidae: *Cuculus canorus* Linnaeus 1758; Capitonidae: *Tricholaema leucomelan* (Boddaert 1783), *Tricholaema melanocephalus* (Cretzschmar 1826); Indicatoridae: *Indicator minor* Stephens 1815; Picidae: *Jynx torquilla* Linnaeus 1758, *Picumnus minutissimus* (Pallas 1782), *Picumnus cirratus* Temminck 1825; *Geocolaptes olivaceus* (Gmelin 1788), *Picoides leucotos* (Bechstein 1803), *Picoides major* (Linnaeus 1758), *Picoides tridactylus* (Linnaeus 1758), *Picus canus* Gmelin 1788; Dendrocolaptidae: *Sittasomus griseicapillus* (Vieillot 1818), *Campylorhamphus pucherani* (Des Murs 1849), *Campylorhamphus trochilirostris* (Lichtenstein 1820), *Campylorhamphus pusillus* (Sclater 1860); Turdidae: *Turdus merula* Linnaeus 1758, *Turdus philomelos* Brehm 1831; Sittidae: *Sitta europaea* Linnaeus 1758, *Sitta carolinensis* Latham 1790, *Sitta krueperi* Pelzeln 1863, *Sitta neumayer* Michahelles 1830, *Sitta tephronota* Sharpe 1872, *Neositta chrysoptera* (Latham 1801), *Tichodroma muraria* Linnaeus 1766; Climacteridae: *Climacteris picumnus* Temminck and Langier 1824, *Climacteris leucophaea* (Latham 1801); Certhiidae: *Certhia brachydactyla* Brehm 1820, *Certhia himalayana* Vigors 1832, *Salpornis spilonotus* Franklin 1831; Rhabdornithidae: *Rhabdornis mysticalis* (Temminck 1825); Emberizidae: *Emberiza citrinella* Linnaeus 1758; Sturnidae: *Sturnus vulgaris* Linnaeus 1758. A much greater number of species was included in the comparative study without being measured.

The horny sheath of the claws in *Archaeopteryx* is sufficiently preserved to study only in a few cases. The most complete set of horny sheaths can be found in the Eichstätt specimen, whereas in the other specimens only one (Berlin) or two (Maxberg, Haarlem) horny sheaths are measurable. We did not see the new (Solnhofen) specimen, but Dr. Wellnhofer kindly sent us photographs of three different claws that seem to be in good condition.

The main purpose of the measurements was to determine the curvature, other features being evident without measuring. We used a method in which only straight lines had to be measured (Fig. 1). The measure of curvature is the angle β. It is constituted by two lines that are tangent to the middle (ideal) line of curvature at the fulcrum point of the joint and at the very tip of the claw, respectively. As can be seen in Fig. 1, $\beta = 180° - \alpha 1 - \alpha 2$. The angles $\alpha 1$ and $\alpha 2$ are different because the assumed ideal line of curvature is, as a rule, asymmetrical. This line can be described with fairly good approximation as being composed of the curves of two quadratic functions that coincide at their vertices. (S in Fig. 1 is the common vertex of both curves.) From the mathematical operations we gain the following result:

$$\alpha 1 = \arctan 2m/xs$$

and

$$\alpha 2 = \arctan - 2m/n - xs,$$

thus

$$\beta = 180° - [\arctan 2m/xs] - [\arctan - 2m/n - xs].$$

RESULTS

TRUNK-CLIMBING SPECIES

The claws of woodpeckers, nuthatches, treecreepers, and other trunk-climbing birds (Fig. 2) match the description given by Yalden (1985) and our prediction. They are comparatively narrow in dorsal view and sharply pointed and strongly curved in lateral view. The majority of the examined specimens exhibit an additional feature that was not predicted: Subapically the palmar (ventral) edge of the claw curves dorsad in such a way that the tip of the claw is more or less distinctly narrowed in lateral (or medial) view. Yalden did not mention this feature, but his drawings of the claws of *Pteropus* Erxleben 1777 and *Dendrocopus* Koch 1816 display a subapical dorsoventral contraction (Yalden, 1985:fig. 1). We did not find this contraction in treecreepers or in some woodpeckers, particularly in the very large species, e.g., *Campephilus* Gray 1840.

The mean value of the curvature of toes II–IV is $\beta = 73.5°$ ($n = 171$; $s = 10.4$) for all trunk climbers. There seems to be a small difference between the species with a stiff, supporting tail ($\beta = 70.8°$; $n = 118$; $s = 9.8$) and those with soft tails ($\beta = 79.4°$; $n = 53$; $s = 9.5$). The intraindividual difference, i.e., the difference between the strongest and the weakest curvature of claws II–IV from any one foot, is low ($\overline{\Delta\beta} = 10.4°$; $n = 58$; $s = 6.2$). The claw of toe I frequently differs from claws of toes II–IV by having a more obtuse angle β. This may be a result of the fact that the first toe is in most species directed more or less caudally and must meet a different strain. Because the claws on the carpal digits of *Archaeopteryx*, if they were climbing tools, would have approached more closely the anteriorly directed toes of modern birds in their mechanical action, the first toes are omitted from comparison in all cases where measurements are concerned.

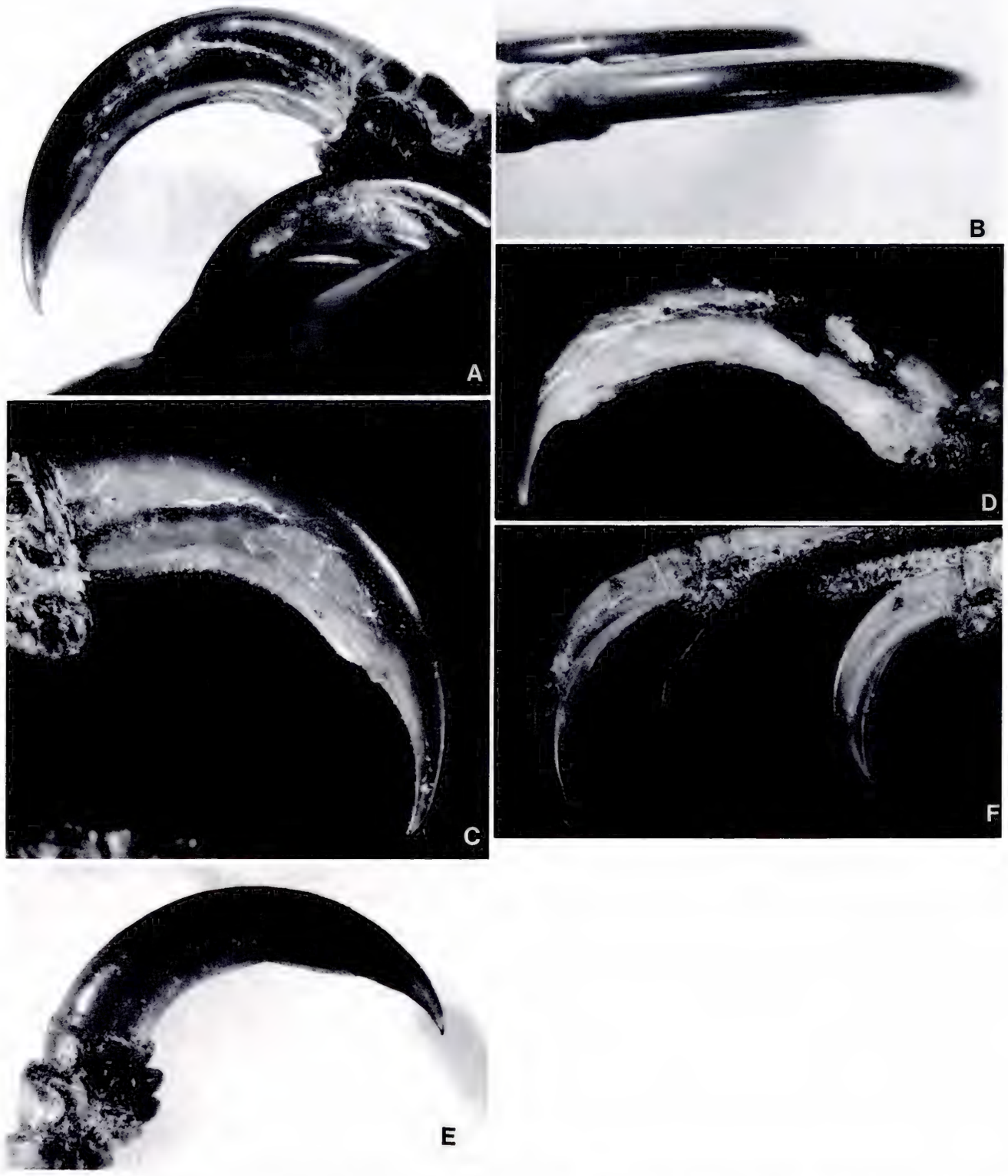

Figure 2. Claws of trunk climbers. **r,** right; **l,** left. **A.** *Melanerpes aurifrons.* Claw r III, in medial view. Note the constricted tip. n = 10.9 mm. **B.** *Melanerpes aurifrons.* Claw r III, in dorsal view. Proximal width of claw, 1.3 mm. **C.** *Picoides major.* Claw l III, in medial view. n = 10.7 mm. **D.** *Picus canus.* Claw r III, in medial view. n = 11.3 mm. **E.** *Campylorhamphus pucherani.* Claw l II, in medial view. n = 6.4 mm. **F.** *Sitta europaea.* Claws r II–IV, in medial view. For claw r III, n = 7.4 mm. For definition of n, see Fig. 1.

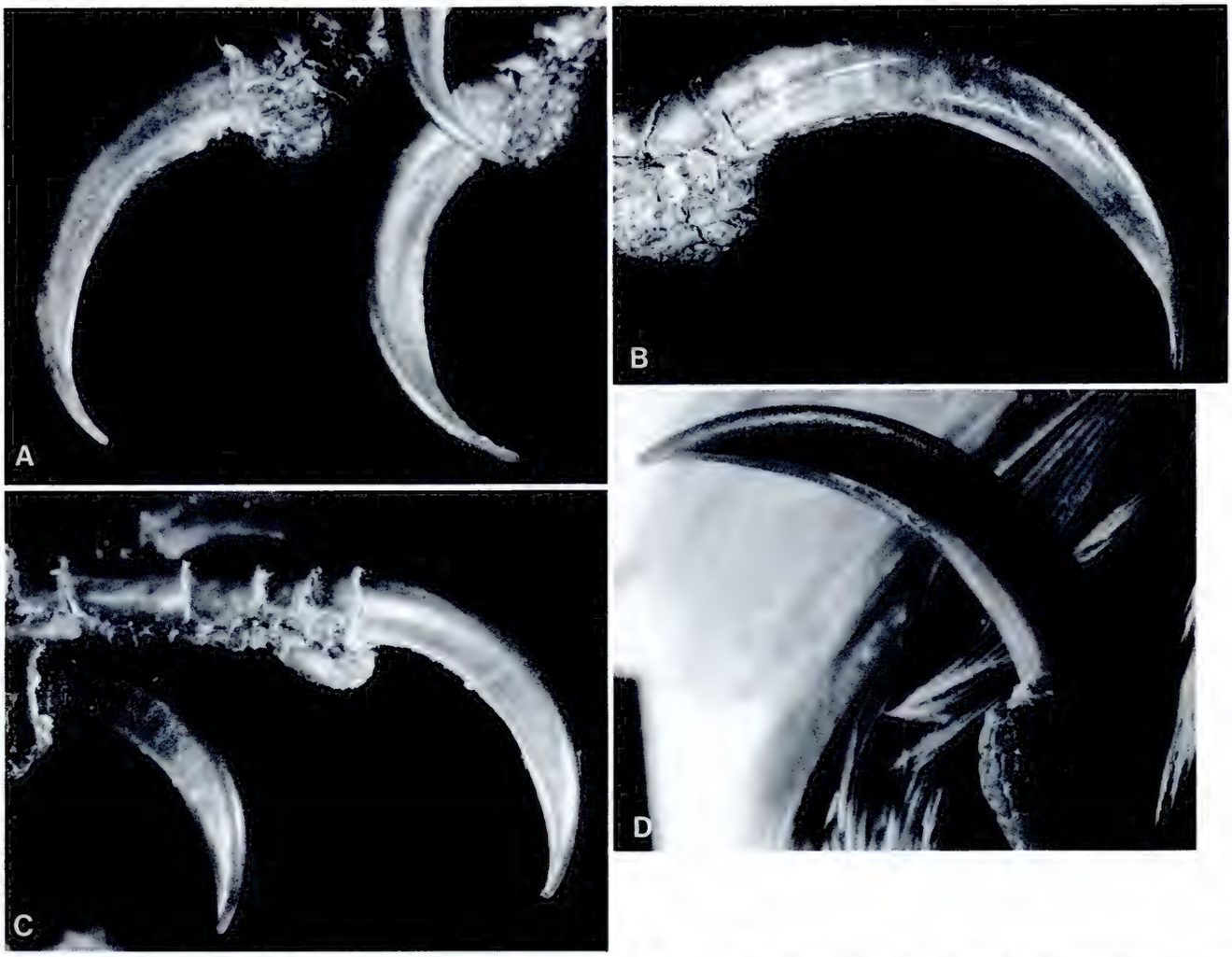

Figure 3. Claws of cliff climbers. **A.** *Sitta neumayer.* Claws r II–IV, in medial view. For claw r III, n = 6.6 mm. **B.** *Sitta neumayer.* Claw l I, in lateral view. n = 8.5 mm. **C.** *Sitta tephronota.* Claws l II–III, in medial view. For claw l III, n = 7.1 mm. **D.** *Sitta tephronota.* Claw r I, in lateral view. n = 9.4 mm.

According to Yalden (1985:92), the ungual phalanges of woodpeckers "are so narrow that they bear lateral grooves where the horny claws are attached to them." However, such grooves are widely distributed and not especially typical of climbing species. They can also be found in birds with broad claws, e.g., rheas, penguins, bustards, rails, screamers, and even in reptiles, e.g., all theropods.

CLIFF-CLIMBING SPECIES

There are very few cliff-climbing species of birds. We examined *Tichodroma muraria* (Wall Creeper), *Sitta neumayer* (Western Rock Nuthatch) and *S. tephronota* (Eastern Rock Nuthatch) (Fig. 3). All of these have claws that are virtually indistinguishable from the claws of trunk climbers, at most with the exception of the tip, which in cliff climbers is only slightly contracted, if at all. The angle β of claws II–IV has the mean value $\beta = 76.1°$ (n = 26; s = 6.7). The average intraindividual difference was $\overline{\Delta\beta} = 7.7°$ (n = 8; s = 3.1). Löhrl (1988) stated that both rock nuthatches do not really climb but, rather, hop ("hüpfen") from one ledge to the next. From our own observations, we got the impression that this kind of hopping is an adequate manner of climbing on a stony substrate.

PREDATORS

The claws of raptorial birds, including owls, are strongly curved, oval or round in cross-section, and conically tapering. The average angle β of claws II–IV is $\beta = 77.5°$ (n = 30; s = 9.9). The intraindividual difference is $\overline{\Delta\beta} = 14.7°$ (n = 10; s = 11.7).

PERCHERS

Perchers, a non-uniform group, comprise birds that are chiefly arboreal but not trunk climbers. Their claws display a great variety of form. In most species, the claws are rather weakly curved ($\beta > 90°$). The claws are lateromedially broader and blunter at the tip than the claws of the three preceding groups. The intraindividual difference is much higher than in climbers ($\overline{\Delta\beta} = 18.7°$; n = 14; s = 5.1). These findings notwithstanding, some species have claws very similar to those of climbers. We found them not only in the "skin-climbing" oxpeckers, but also in species that, as a rule, do not climb anywhere, e.g., the Hoatzin

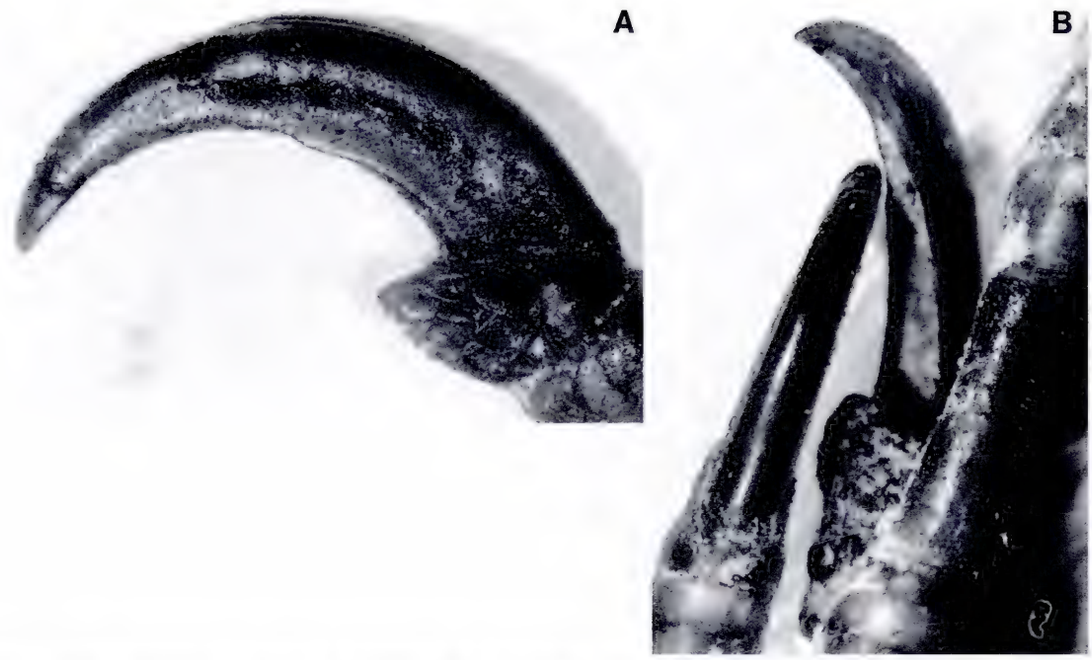

Figure 4. Claws of *Cuculus canorus*. **A.** Claw r II, in medial view. $n = 6.4$ mm. **B.** Claws r II, in dorsal view and r I in ventral view. Proximal width of claw II, 1.3 mm.

and many cuckoos (Fig. 4). We can also confirm Yalden's (1985) observation that tree-swifts (Hemiprocnidae) have woodpecker-like claws.

OTHERS

Another group embodies mostly swimming and ground-dwelling species. Their claws are predominantly plump and blunt, with a very obtuse angle β. Even in this group, however, strongly curved, sharply pointed, and comparatively narrow claws can be found. This is the case, for instance, in the Cariamidae, Stercorariidae and in *Fratercula arctica* (Linnaeus 1758) (Fig. 5). Usually only the second toe has such a sickle-shaped claw.

ARCHAEOPTERYX

The carpal claws of *Archaeopteryx* (Fig. 6) differ from the claws of the toes in being longer and more strongly curved. The intraindividual difference in the only specimen for which it could be determined is surprisingly high (Table 1). There is no dorsoventral contraction at the claw tip. Considering just the outline, the claws of the fingers are most similar to the claws of cliff-climbing birds (Fig. 7).

The horny claws of *Archaeopteryx* are remarkably gracile. Their lateral and medial walls are extremely thin, in contrast to the thickened slat-like dorsal part. In life, their cross-section may have approached the construction of a T-girder. The horny part of the sheath does not reach as far proximally as in modern birds. Appropriate drawings illustrating this feature were given by Wellnhofer (1974) and Yalden (1985). The horny sheath slipped off the terminal bony phalanges of digitus alulae of the Haarlem specimen and of digitus minor of the Eichstätt specimen (Fig. 6B). Without their bony filling, the sheaths do not seem to be strong structures.

MAMMALS

We took measurements of the claws of 11 species of mammals and examined many more without measuring them. In concurrence with Yalden's (1985) results, we found that the claws of many climbing species are similar to the claws of climbing birds in mechanical respects; however, we found many exceptions, e.g., the primates. Also, some species that do not climb very regularly, such as lions and tigers, have claws displaying the canonical construction of climbers. Thus, the data on mammalian claws did not add any new aspects to our study and will be omitted from further consideration.

DISCUSSION

Our results indicate that climbing birds tend to have a particular construction of claws. The main selective force seems to ensue from the mechanical constraints attached to climbing on more or less vertical surfaces, whereas the material of the substratum appears to be of minor importance. This is demonstrated by the negligible difference between the claws of trunk climbers and those of cliff climbers. In trunk-climbing species, the claw can penetrate the substratum, but in cliff climbers it cannot. Hence, in trunk climbers the tip of the claw is very often constricted as a result of wear, but rarely and weakly so in cliff climbers. The constriction of the tip is obviously a result of differential abrasion. The dorsal layer of the horny sheath is more massive and thicker than the lateral and ventral parts. It may be that in the tiny treecreepers, in which we could not find constricted tips, the claws do not penetrate the bark. We cannot say much about other trunk-climbing birds lacking the constriction, but it would seem to be a worthwhile project to analyze someday whether or not any correlation exists between the extent of constriction in claws and the kinds of trees preferred by the climbers.

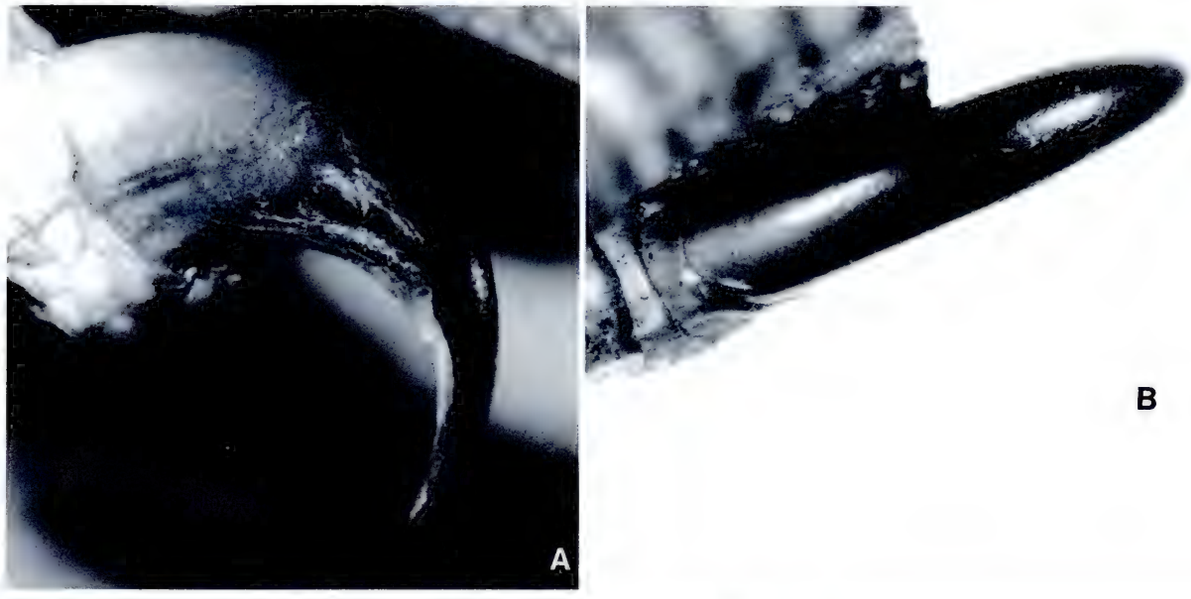

Figure 5. Claws of *Fratercula arctica*. **A.** Claw r II, in medial view. n = 9.3 mm. **B.** Claw l II, in dorsal view. Proximal width of claw, 1.8 mm.

Thus far the prediction regarding the constructional properties of claws used mainly for climbing has been confirmed. However, this particular construction apparently is not exclusively specific to climbing species. It is certainly not surprising to find similar claws in the oxpeckers, which frequently climb, even if on a giraffe's neck instead of on cliffs or trees. But we have no convincing explanation for why many cuckoos and other birds have similar claws, and we shall not try to find one in this article. We simply must take notice of the fact that several functions obviously can be fulfilled with claws built exactly like the claws of climbers. Knowing this, one can no longer assert with confidence that the claws of *Archaeopteryx* were used mostly for trunk climbing, even if they were constructed precisely like woodpecker claws.

Even so, the claws of *Archaeopteryx* are not constructed like those of woodpeckers. When examined carefully, they reveal some small but noteworthy peculiarities. The most striking one is their weakness. At least the proximal third of the sheath apparently consisted of soft tissue; hence, the hold of the horny sheath on the underlying bony phalanx must have been much weaker than in the claws of extant birds. In spite of being thin, the horny sheath does not display any sign of wear. The destruction apparent in some claws seems to be a result of imperfect postmortem preservation. The high intraindividual range of the degree of curvature seen in *Archaeopteryx* may indicate that no strong selective force acted in favor of an optimal shape for climbing. All facts considered, it is difficult to imagine that the gracile claws of *Archaeopteryx* should nevertheless have been used many times a day for this purpose. Incidental clambering or clinging to a trunk or a cliff cannot be precluded, but nothing beyond this. In the toes, the weak curvature alone prevents the claws from being efficient climbing hooks.

We must admit that we do not know at all for what *Archaeopteryx* could have used its carpal claws. It may be that Stephan (1987) is right in maintaining that these claws were still present because they were simply not yet eliminated by selection. On the other hand, there might be good reasons for the perpetuation of otherwise useless claws as a means of protecting the tips of the digits, as is demonstrated by carpal claws of numerous modern birds. Thus, the carpal claws of *Archaeopteryx* may be interpreted as a combined result of phylogenetic legacy and constructional constraints.

Other supposed functions of the claws are grasping (Ostrom, 1976; Thulborn and Hamley, 1985) and grooming (Rietschel, 1985). However, both of these functions seem to be incompatible with the size and arrangement of primaries and other feathers. Some more imaginable and not too unrealistic functions are menacing displays, fighting, and clasping during copulation.

But it may be that the claws had a function too odd to be reconstructed using our current knowledge of living birds. Consider the numerous features of modern animals that we understand only because we have the opportunity to study the behaviour of the living organisms.

The last point to be discussed, we are afraid, should logically have been the first one. It concerns the forest so badly needed by trunk-climbing gliders. To the best of our knowledge, this forest did not exist in the habitat occupied by *Archaeopteryx*. According to de Buisonjé (1985:62), in the "Solnhofen area . . . an almost rainless strip existed along the northwestern coast, comparable with the present-day's Namib desert . . ." Less arid, but still semiarid conditions could have prevailed in mountain slopes ". . . well outside the vicinity of the Solnhofen backreef basin." This would also help explain the diversified insect fauna preserved in the Solnhofen limestones, inasmuch as semiarid, steppe-like environments with temporary freshwater pools are usually rich in insects. According to Viohl (1985:41), ". . . the Solnhofen Lithographic Limestones do not provide any evidence for trees. . . . Major continuous forests were surely missing. The main vegetation was probably a bushland of conifers and Bennettitales alternating with open plains, with only sparse vegetation." To cut a long story short, if the claws of *Archaeopteryx* were an adaptation for trunk climbing, they would have been a strange extravagance for an animal living in a treeless habitat.

Figure 6. Claws of *Archaeopteryx lithographica*. **A.** Claw manus r I, in lateral view. $n = 9.8$ mm. **B.** Claw manus l III, in lateral view. Note the dislocated horny sheath. $n = 5.1$ mm. **C.** Claw pes l IV, in lateral view. $n = 7.0$ mm.

REMARKS ON THE BEGINNINGS OF BIRDS

The early history of birds is in part the early history of bird flight. In what has frequently been a very confused discussion concerning this matter, the problems of the origin of flight are often reduced to the two alternatives of "trees down" versus "ground up." In this way, the real problem is obscured. The development of flight is primarily a question of the energetically powered organismic apparatus and of aerodynamics, and not of the ecological circumstances (Peters and Gutmann, 1976, 1985; Padian, 1985). Most authors considering the origin of flight in this way agree that flapping flight as the first stage of flight is highly improbable, if not impossible. The first flight must have been gravity-assisted (Bock, 1965, 1986; Clark, 1976; Peters and Gutmann, 1976, 1985; Peters, 1984, 1985; Norberg, 1985; Rayner, 1985a, 1985b; and others; see extensive bibliography in Stephan, 1987). Hence, the early birds had to jump from some kind of elevated site. From the aerodynamic point of view, it makes no difference whether the elevated starting point is a tree or a big stone or a cliff ledge. We still prefer the "rocky" version, not precluding, however, that prebirds, and *Archaeopteryx*, could perch in bushes as long as they could reach the branches bipedally (Peters, 1984).

The arboreal theory *sensu stricto* demands a lot from prebirds. They had to change, for unknown reasons, from bipedal cursors to quadrupedal climbers. (At the time, they did not yet know that they would become flyers.) They had to climb with limbs unsuitable for this mode of locomotion. They had to evolve the very specific construction of wings for flight against the selective forces acting in favor of limbs appropriate for climbing, which are very different from wings. These selective forces must be taken as certain because climbing was at least as important for survival as was primitive flight. Without climbing, the "arboreal" prebird could not even begin to fly.

Bock (1986:63) incorrectly quotes Peters (1984, 1985) as maintaining that "*Archaeopteryx* already possessed the specialized linkage system in the wing which extends and flexes the lower arm and hand simultanously." Taking into consideration what

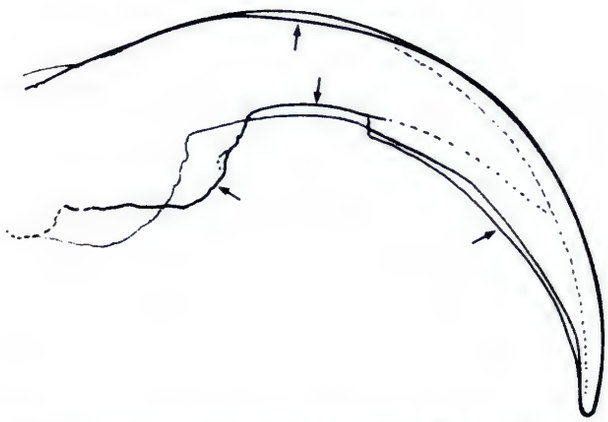

Figure 7. The outlines of the claws from Figs. 3B and 6A, brought to the same size and combined. Arrows indicate the claw of *Archaeopteryx*.

Table 1. The angle β (measure of curvature) of the claws of *Archaeopteryx*. Abbreviations: l, left; r, right.

Specimen	Manus	β	$\bar{\beta}$	Pes	β	$\bar{\beta}$II–IV
Eichstätt	r I	80.9°		r I	92.7°	
	r II	84.3°		r II	75.6°	
	r III	60.4°		r III	91.7°	
				r IV	97.7°	
	l I	54.4°		l I	59.9°	
	l II	76.6°		l II	100.0°	
	l III	88.2°*		l III	79.4°	
				l IV	77.0°	
Haarlem	l III	65.5°				
Solnhofen	r I	78.0°				
	l I	97.7°				
	l II	65.0°				
			75.1°			79.5°

* Horny sheath dislocated, measurement probably inexact.

can be inferred from the osteological construction, we agree with Stegmann (1937) that *Archaeopteryx* did not yet possess this system. The point is that, regardless of whether *Archaeopteryx* possessed it or not, this linkage system could not evolve in a limb used for climbing because the limb could not be improved as a wing as long as it was a climbing instrument, and it could not stop climbing as long as it was not improved as a wing. From the viewpoint of functional morphology, a "climbing wing" in the ancestors of modern birds is a "contradictio in adjecto."

All of these difficulties and contradictions are avoided in a hypothesis ironically called the "ground down" theory by Olson (1987). I venture to use this term, which shows that irony is often very close to the serious facts. According to this hypothesis, the prebird was a bipedal cursor living in a rugged or mountainous habitat with cliffs and boulders. The evolutionary sequence of jumping, gliding, and active (flapping) flight could evolve quite easily and without all of the difficulties of climbing and exact landing that the arboreal hypothesis must explain. In his last paper on this subject, Peters (1985) was puzzled by the seeming significance of the claws of *Archaeopteryx* as a climbing device. With our new data, the claws are still a puzzle, but they are no longer an irrefutable proof of trunk climbing.

SUMMARY

We tested the hypothesis that narrow, curved, and sharply pointed claws are not confined to trunk climbers by studying the claws of *Archaeopteryx* and many extant birds representing different systematic and ecologic groups. The claws of *Archaeopteryx* and 38 extant species were measured to determine the curvature. These are the results: The claws of trunk climbers and cliff climbers are narrow lateromedially and sharply pointed; the angle β as a measure of their curvature (Fig. 1) averages about 75°, and the intraindividual difference of this angle is low (ca. 9°). In most trunk-climbing species, but not in cliff climbers, the tips of the claws are narrowed in lateral (or medial) view. Other differences between the claws of trunk climbers and cliff climbers are negligible.

The claws of the majority of non-climbing species are clearly different from the claws of climbers. However, in non-climbing species of some groups, e.g., cuckoos, skuas, all or some of the claws are very similar to the claws of climbers. These findings and the great similarity of the claws in trunk climbers and cliff climbers corroborate the previously mentioned hypothesis.

The superficial outline of the carpal claws of *Archaeopteryx* strongly resembles that of the claws of cliff-climbing species. A closer inspection, however, reveals important differences: The horny sheaths of the claws of *Archaeopteryx* are very weak, they cover at most the distal two-thirds of the bony phalanges, and the intraindividual difference of angle β is rather wide.

We conclude that the claws of *Archaeopteryx* could not be used routinely for climbing. But, according to our results, even if they were built exactly like claws of climbers, they cannot be taken as an unmistakable indication of a trunk-climbing function. This conclusion coincides with the fact that *Archaeopteryx* lived in a treeless habitat. At present, the carpal claws of *Archaeopteryx* seem to be best explained as the combined outcome of phylogenetic legacy and constructional constraints.

Our results are relevant for hypotheses pertaining to the origin of flight. If early birds such as *Archaeopteryx* cannot be regarded as trunk climbers, the hypothesis that birds began to fly on slopes or ridges gains additional support.

The conceptive guideline for this investigation was an organismic version of evolutionary theory that claims the primacy of construction and "internal" selective forces over external (ecological) functions and their effects.

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We are deeply indepted to G. Viohl, Jura-Museum Eichstätt, for the opportunity to study the casts of some *Archaeopteryx* specimens, to P. Wellnhofer for sending us photographs of the claws of the sixth specimen of *Archaeopteryx*, and to K. Padian for help in correcting our English text and offering many useful suggestions.

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A NEW ORDER OF BIRDS (CLASS AVES) FROM THE LOWER CRETACEOUS OF SPAIN

J. L. Sanz and José F. Bonaparte

ABSTRACT. We describe a new, small, articulated fossil bird from the Lower Cretaceous (probably Hauterivian–Lower Barremian) of Las Hoyas, Provincia Cuenca, Spain, as *Iberomesornis romerali* new genus, new species. We propose that this taxon represents a new order of birds, the Iberomesornithiformes. The specimen presents a striking combination of primitive and derived characters. Eight apomorphic characters are shared with the Ornithurae: reduced cervical neurapophyses, fused cervical ribs, reduced number of dorsal vertebrae, presence of a pygostyle, gastralia absent, strut-like coracoid, furcula with a developed hypocleidium and low clavicular angle, and ulna longer than humerus. Two vertebral autapomorphies characterized *Iberomesornis*, which appears to be the sister-group of the Ornithurae. The sacrum, pelvic girdle, and hindlimbs of *Iberomesornis* are primitive and generally similar to those of *Archaeopteryx* and theropod dinosaurs. Based on the characters of *Iberomesornis*, we suggest that the early evolution of birds from *Archaeopteryx* was first concentrated in the pectoral girdle, forelimb, and pygostyle to achieve the structural requirements for active flight.

RESUMEN. Se describe una pequeña nueva ave fósil articulada procedente del Cretácico inferior (probablemente Hauteriviense–Barremiense inferior) del yacimiento de Las Hoyas, provincia de Cuenca, España. Se propone para esta nueva forma aviana la denominación *Iberomesornis romerali* n. gen., n. sp. Se sugiere que este taxon representa un nuevo Orden de Aves, los Iberomesornithiformes. El especimen presenta una sorprendente combinación de caracteres primitivos y derivados. Ocho rasgos apomórficos son compartidos por los Ornithurae: neurapófisis cervicales reducidas, costillas cervicales fusionadas, número reducido de vértebras dorsales, presencia de un pigostilo, gastrales ausentes, coracoides en forma de puntal, fúrcula con hipocleidio desarrollado y bajo ángulo clavicular y ulna más larga que el húmero. Dos autapomorfías vertebrales caracterizan a *Iberomesornis*, que aparece como el grupo hermano de los Ornithurae. El sacro, cintura pélvica y extremidades posteriores de *Iberomesornis* son en general primitivos, semejantes a los de *Archaeopteryx* y dinosaurios terópodos. En base a los caracteres de *Iberomesornis* se postula que la evolución temprana de las aves a partir del nivel de *Archaeopteryx* se concentró primeramente en la cintura pectoral, extremidad anterior y pigostilo, para alcanzar los requisitos estructurales necesarios para el vuelo activo.

Key words: Aves, Lower Cretaceous, Spain, *Iberomesornis*.

INTRODUCTION

After the discovery of *Archaeopteryx* in the middle of the last century, and its immediate recognition as representing the most primitive stage of avian evolution, there have been few significant finds linking that primitive form to later birds (Kurochkin, 1985a, 1985b). The new specimen described herein from the Lower Cretaceous of Spain is exceptional in that it illustrates just such an intermediate stage between *Archaeopteryx* and later birds.

The locality of Las Hoyas, which produced the specimen, is Neocomian in age (probably Hauterivian–Lower Barremian; Vilas et al., 1982). It has provided a diversified flora and fauna, notable for a broad representation of fishes, especially primitive teleosteans, amphibians, one turtle and one lizard (Sanz et al., 1988b). The Las Hoyas site is comparable to other localities that were situated in the European area of Tethys from the Late Jurassic to the Early Cretaceous. These include well-known sites such as Solnhofen, Canjuers, and Cerin or Montsech and represent lacustrian or lagoonal depositional environments. The Las Hoyas outcrop comprises a lithographic limestone that has permitted the preservation of delicate structures such as insect wings and a bird feather (Sanz et al., 1988a).

The association of the feather and the new bird described herein is likely, based on two arguments: (1) the avian level of derivation of the Las Hoyas specimen is greater than that of *Archaeopteryx*, which was feathered, and (2) comparable avian bone remains are known from Montsech (Lacasa, 1986), and these include evidence of feathers.

The purpose of this paper is to describe the morphology of the new Cretaceous bird in order to evaluate its phylogenetic relationships and its taxonomic and evolutionary significance. We think that this new taxon provides some outstanding new information concerning the anatomical attainments preceding the evolutionary radiation of modern birds, the functional improvements in flight capability over that of *Archaeopteryx*, and the evaluation of differential evolutionary rates from the *Archaeopteryx* level.

SYSTEMATICS

Class Aves Linnaeus 1758

Iberomesornithiformes new order

TYPE FAMILY. Iberomesornithidae new family.

DIAGNOSIS. Bird with pectoral region comparable to that of Ornithurae and with the pelvis and posterior limbs similar to that of *Archaeopteryx*. Cervical vertebrae with no traces of

neurapophyses. Dorsal vertebrae number 11, with relatively high neural arches and laminar spines. Sacral vertebrae number five, with hypapophyses. Free caudal vertebrae number eight, with incipient procoely, the three anterior ones with broad transverse processes. Pygostyle laminar, formed of about 10–15 vertebrae. Gastralia absent or vestigial. Coracoid strut-like with a broad sternal expansion for contact for the sternum. Furcula with developed styloid hypocleidium and relatively low clavicular angle. Sternum ossified, articulated with five visible sternal ribs. Humerus/ulna length ratio is 0.94. Proximal and distal tarsals and metatarsals unfused. Hallux reverted, with hypertrophied ungual phalanx.

REMARKS. The order Iberomesornithiformes comprises birds anatomically intermediate between *Archaeopteryx* and later birds. They are characterized by the presence of highly derived avian forelimbs and pectoral girdle, contrasting with a generally primitive, *Archaeopteryx*-like hindlimb and pelvic girdle. The 11 dorsal vertebrae are intermediate in number between what is found in *Archaeopteryx* and Ornithurae. The ilium is probably primitive, with its preacetabular surface greater than the postacetabular surface. The ischium does not present any of the peculiarities of *Archaeopteryx*.

Iberomesornithidae new family

TYPE GENUS. *Iberomesornis* new genus.
DIAGNOSIS. As for order.

Genus *Iberomesornis* new genus

TYPE SPECIES. *Iberomesornis romerali* new species.
DIAGNOSIS. As for order.
ETYMOLOGY. *Ibero,* for the Iberian Peninsula; *mesornis,* Greek, intermediate bird; masculine.

Iberomesornis romerali new species

Figures 1–5

HOLOTYPE. Almost complete, articulated individual, preserved in left lateral view, without skull, anterior cervicals, both carpometacarpi and all carpal digits. Specimen LH022R, Unidad de Paleontología, Departamento de Biología, Facultad de Ciencias, Universidad Autónoma de Madrid.
DIAGNOSIS. As for order.
TEMPORAL AND GEOGRAPHIC DISTRIBUTION. Neocomian, probably Hauterivian–Early Barremian. Las Hoyas, La Cierva Township, Province of Cuenca, east-central Spain.
ETYMOLOGY. In recognition of the discoverer of the specimen, Mr. Armando Díaz Romeral, resident of Cuenca, Spain.
DESCRIPTION. The holotype, which lacks the skull and anterior and middle cervical vertebrae (Figs. 1–5), is exposed in left lateral view and is relatively well articulated, especially the preserved parts of the vertebral column. It was found in two lithographic slabs, weathering of which affected some regions, e.g., the pelvis. Both slabs were joined for the final preparation of the specimen. No carpal digits are preserved, but their absence may not be a result of weathering or erosion. Fracturing effects are observed in some appendicular bones, with slight displacement in some of them.

The holotype is a small specimen, probably adult, with a 15-mm-long femur and a 19-mm-long humerus. The length of the preserved vertebral column is 57 mm, and the whole estimated length of the specimen is about 70–80 mm.

The preservation of the specimen is satisfactory, and the delimitation of the pieces is relatively clear in general, although there has been some deformation by compaction of the sediments.

Axial Skeleton. *Cervical Vertebrae:* The last four articulated cervicals are preserved, revealing a posterior curvature to the neck and two somewhat different morphological types of cervicals. The anteromost two preserved cervicals are relatively elongated, without any evidence of neural spines, and with a long, clear, bony ridge linking the pre- and postzygapophyses laterally. The other two cervicals are shorter, and they have neither bony ridges nor developed neurapophyses. Some traces of opisthocoely are present in the two anterior vertebrae, but not in the others. The cervical centra are excavated laterally, but without any evidence of pleurocoels. Cervical ribs and fused diapophyses and parapophyses seem to be present in the last cervicals. An absence of neural spines is a highly derived feature in relation to *Archaeopteryx* (Wellnhofer, 1974; Ostrom, 1976), and the lack of heterocoely indicates that the vertebral centra of *Iberomesornis* are more primitive than those in modern birds.

Dorsal Vertebrae: We consider the first dorsal vertebra to be the first one with a well-developed neurapophysis, diapophyses in dorsal position, and a clearly different morphology in relation to the last cervical. Eleven dorsal vertebrae can be identified, with little regional differentiation. The centra are relatively low and elongated; in general, they are a little longer than those of the last cervicals. The lateral surfaces present slight depressions, recalling the condition in Theropoda *sensu* Romer (1964). The neural arch is high, with well-defined zygapophyses. The prezygapophyses extend beyond the anterior edge. From the 4th dorsal posteriad the diapophyses are elevated to the level of the zygapophyses. Beginning with the 5th dorsal, the parapophyses seem to be situated on the neural arch. Proceeding caudad the parapophyses appear to migrate dorsad in successive vertebrae. The neural spine is laminar, axially broadened, and rather low, recalling the primitive condition in forms such as *Lagosuchus* Romer 1971 (Bonaparte, 1975) and *Compsognathus* Wagner 1861 (Ostrom, 1978), although the neural arch in *Iberomesornis* is quite a bit higher as a result of its noticeable neural pedicles. We consider this character to be derived (autapomorphic) in relation to the condition observed in *Archaeopteryx* and later birds.

The presence of 11 dorsal vertebrae in *Iberomesornis* is an intermediate (derived) character between Coelurosauria—*Archaeopteryx* (13–14 dorsals; Ostrom, 1976) and extant birds (4–6 dorsals; Van Tyne and Berger, 1976).

Sacral Vertebrate: The sacral vertebrae are firmly attached to one another, but they are not intimately fused. They number five, although we admit the possibility that the last dorsal and the two anterior caudals could function as part of the sacrum. There is no evidence of co-ossification, however. The distinction between the last sacral and the first caudal vertebra is very clear. The centra of the sacral vertebrae *sensu stricto* show evidence of axial, keel-like ventral processes (hypapophyses). A "rounded median keel" is reported by Seeley (1876) in the sacral vertebrae of *Enaliornis* Seeley 1876. *Enaliornis* is considered by Cracraft (1984) to be close to some diving birds, baptornithids plus hesperornithids, or the latter plus loons and grebes. The number of five sacral vertebrae coincides with Ostrom's (1976) observations for *Archaeopteryx,* and *Iberomesornis* is persistently primitive in this regard.

Free Caudal Vertebrae: Eight consecutive free caudal vertebrae can be observed; the three anterior ones are exposed mainly in ventral view, and the remainder in lateral view. The last free caudal vertebra articulates with the pygostyle. The centra of the free caudal vertebrae are short, with a faintly convex posterior

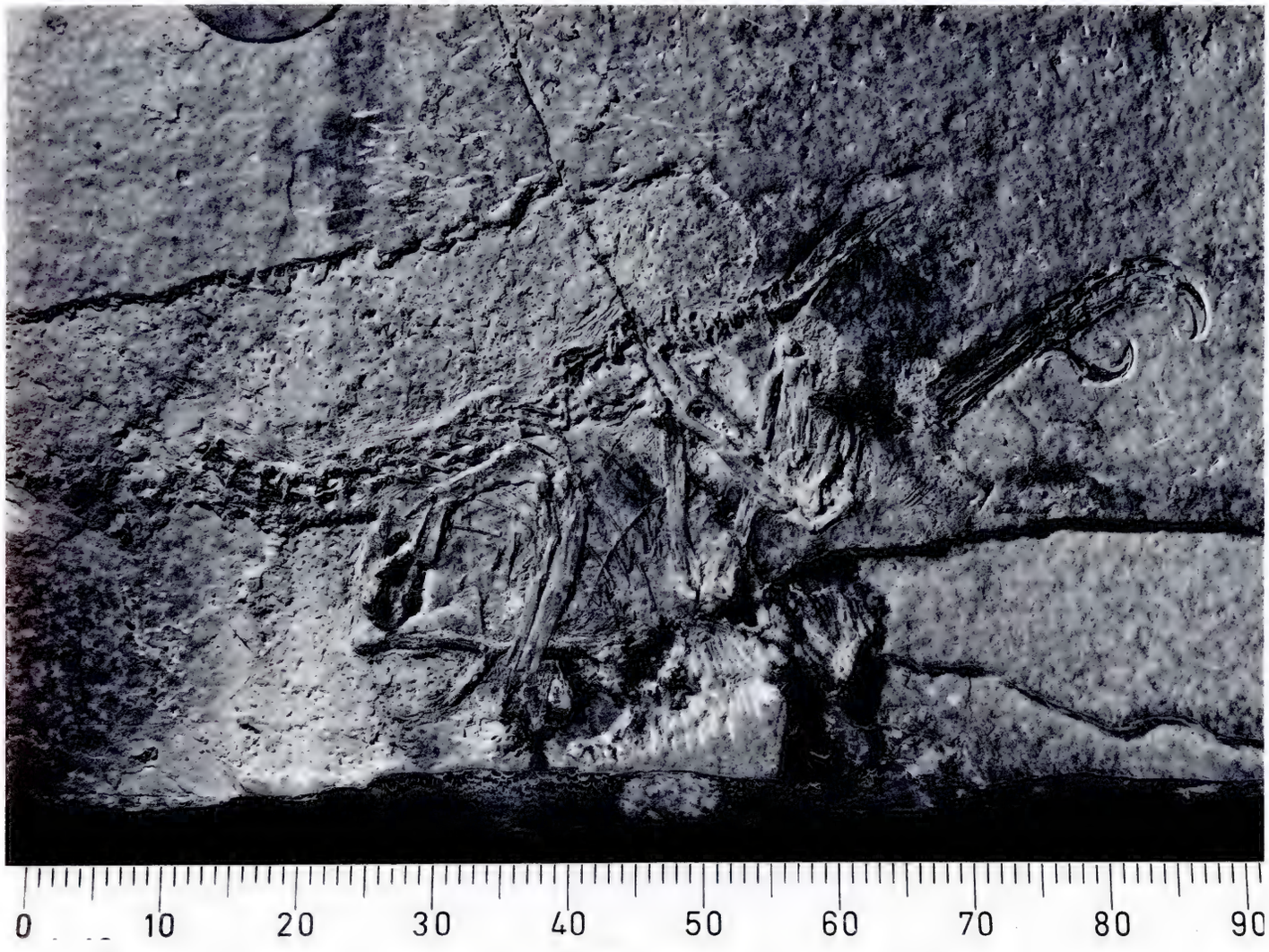

Figure 1. *Iberomesornis romerali* n. gen., n. sp. Specimen LH022R. Lower Cretaceous of Las Hoyas (Cuenca, Spain).

end and a slightly concave anterior end. The ventral edge presents an axial cleft limited by two flanges, and the lateral side has a well-defined depression.

Postmortem distortion of the three anterior caudal vertebrae makes their interpretation difficult, although it can be seen that the transverse processes were broad. Well-developed postzygapophyseal processes that extend beyond the posterior edge are observed in the last caudals. No neural spines have been observed in the free caudals, and haemapophyses are present from the 4th caudal vertebra posteriad.

The small number of free caudal vertebrae is a derived character relative to that in *Archaeopteryx*, and it is similar to that of extant birds.

Pygostyle: This bone has been preserved almost in its entirety, except for the most distal region, which is represented by a mold in the limestone surface. Anteriorly, three or four fused vertebrae are distinct, but posteriorly individual vertebrae cannot be distinguished. We estimate the total vertebral number of the pygostyle to be about 10–15. The ventral outline is slightly concave in lateral view, and the dorsal outline is slightly convex. We infer from our observations that its transverse section must be narrow and deep.

The presence of a pygostyle in the Neocomian bird is a derived character relative to *Archaeopteryx* and the Theropoda, and it represents the oldest record of this bone among birds.

Ribs: The evidence for cervical ribs is very limited. There are traces of free ribs extending from the anterior cervical vertebrae, and they should be fused to the vertebral centra in the posterior cervical vertebrae. The dorsal ribs, many of them in articulated position, are bicipital, with the tuberculum less developed than the capitulum. They are long, elliptical in cross-section, and without any overlapping (uncinate) processes. Most of the dorsal ribs would appear to have articulated with the sternal ribs.

Sternal Ribs: Five sternal ribs are joined to the lateral edge of the sternum. They are short, faintly expanded at their extremes, well ossified, and oriented dorsoposteriorly, forming a broad angle as they join the dorsal ribs. Two whole ribs and three partially exposed ribs, the latter in part covered by the radius, are observed in front of the left radius.

Gastralia: No certain evidence indicates the existence of gastralia, although the broadly developed sternum and the presence of five sternal ribs could be an indication of their absence. If that is the case, then sternal development would imply an evolutionary reduction or loss of gastralia.

Figure 2. *Iberomesornis romerali* n. gen., n. sp. Ultraviolet-induced fluorescence photograph of LH022R.

Sternum: A portion of the sternum where five sternal ribs articulated is preserved. It could represent the right lateral half (medial view) or the left lateral half (lateral view). The presence of a sternal keel is uncertain. The anterior edge of the sternum is not visible, but it could have reached the coracoids.

Shoulder Girdle. The left scapula and coracoid have been preserved articulated and are approximately in their original position. The scapula has a transverse fracture at about the middle of the scapular blade, and it is partially covered by the humerus. The right coracoid has its distal half preserved. The furcula is almost complete, exposed in anterior or ventral view and articulating via its left branch or arm with the coracoid. The three shoulder girdle bones of *Iberomesornis* show very well-defined avian characters.

Scapula: The scapula is long, narrow, and slightly arched. The region adjoining the coracoid is covered in part by the humerus, as is a large portion of the distal region of the blade. The proximal half of the blade is narrow, extremely flat, and faintly convex, but the distal half seems to be somewhat concave. The dorsal vertebra near the expanded scapular blade cannot be recognized because of the incomplete preparation of the specimen. The scapula would not appear to have reached the 8th dorsal vertebra.

Coracoid: The left coracoid is exposed in latero-anterior view. It has a broad sternal expansion, and the medial and humeral regions are narrow and rather slender. The humeral region is represented by a cast on the counterpart slab that is difficult to interpret. However, the existence of a lateral protuberance of the glenoid region and the coracoid head outline, including the coracohumeral surface, can be verified. The coracoid expands sternally, with a broad sternal facet that is more or less straight. The presence of a sternocoracoidal process appears to be likely, although evidence for it is unclear.

In general, the structure of the entire coracoid is basically avian in aspect, and it is highly derived relative to that of *Archaeopteryx*.

Furcula: The furcula is almost complete. It has a marked styloid furcular process in anterior view, probably for ligaments attaching to the sternum. The angle between both clavicles is about 60°, noticeably smaller than in *Archaeopteryx* (Ostrom, 1976). The clavicles are relatively long and rather slender, with a slight dorsoventral convexity and a thinner aspect in the region

Figure 3. *Iberomesornis romerali* n. gen., n. sp. Ultraviolet-induced fluorescence photograph of LH022R. Abbreviations: **f,** furcula; **lc,** left coracoid; **lh,** left humerus; **lu,** left ulna; **rf,** right femur; **rt,** right tibia.

adjoining the furcular process or hypocleidium. The proximal ends of the clavicles have no notable morphological features.

The articulation of the furcula with the medial edge of the coracoid can be noted. The structure of the furcula and coracoids of *Iberomesornis* represent an evolutionary stage that probably indicates a flight capacity similar to that of extant birds. This is one reason why the evolutionary distance between *Iberomesornis* and *Archaeopteryx* is so great.

Forelimb. The left humerus has been preserved in near articulation with the radius and ulna. There are no traces of the carpus or manus. The humerus is shorter than the ulna, which is the converse of the condition seen in *Archaeopteryx*. The humerus/ulna length ratio is 0.94. The greater forearm length is interpreted as being evolutionarily more derived than that of *Archaeopteryx* (1.11–1.16 humerus/ulna length ratio; Wellnhofer, 1974) and more similar to that of extant birds and the Enantiornithes.

Humerus: The humerus is exposed in ventrolateral view, oriented in an elevated, posterior position. It has two fractures that affect the continuity of the diaphysis. The head is probably in articular position, but no major anatomical details are visible in this region. The most noticeable proximal structure is the deltoid crest, which shows continuity with the internal tuberosity and the head of the humerus. There should also be a continuity between the internal tuberosity and the humeral head. The bicipital depression is slight, and it is not possible to observe the existence of a pneumatic foramen because of the position of the bone. Nevertheless, the pneumatic condition of the bone is evident in the middle of the diaphysis. The distal position is slightly broadened, and there are no remarkable features in the condylar region. The ventral side is concave in both directions, and neither condyles nor intercondylar depression are observed. However, we note that the entepicondyle is placed more distally than the ectepicondyle and that the distal end emerges in an oblique position, recalling the condition in Enantiornithes (Walker, 1981).

Even though the preservation of the humerus is not optimal, we interpret the bicipital depression, proximal tuberosities, and lack of definition of the distal condyles as implying a primitive state, more primitive than that of the Enantiornithes and later

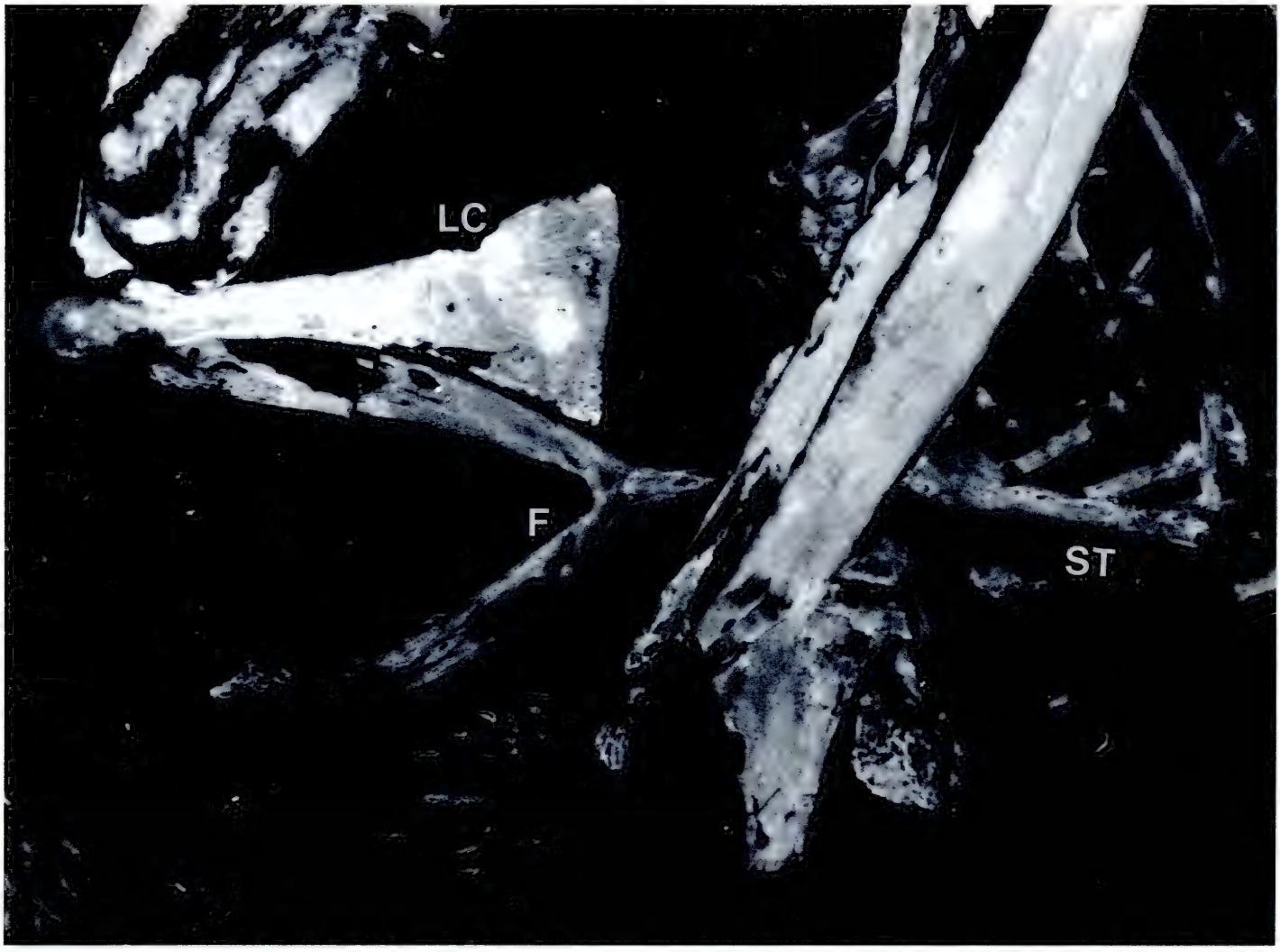

Figure 4. *Iberomesornis romerali* n. gen., n. sp. Ultraviolet-induced fluorescence photograph of LH022R. Abbreviations: **F,** furcula; **LC,** left coracoid; **ST,** sternum.

birds. At the same time, it is similar, in general, to the humerus of *Archaeopteryx* (Ostrom, 1976).

Radius and Ulna: The radius and ulna are almost articulated with the humerus. The radius shows some fractures in its proximal half. It is in general slender but slightly expanded at its ends. The ulna has a broken and removed distal end. It is much thicker than the radius, with a curved posterior outline. The proximal region is faintly curved anteriorly. The olecranon is poorly marked and the articulation for the humerus is broad. A lateroproximal process, which is separated from the olecranon by a depression, must be the projection of the external condyle. We cannot interpret the distal end with certainty because it is displaced, but it does show a sharp flange on the external condyle and an adjacent depression.

No rugosites suggesting feather insertions can be noted. The posterior curvature of the ulnar outline, a feature evaluated by Gauthier (1986) in the Archosauria, does not differ from that of *Archaeopteryx* and later birds.

Pelvic Girdle. The left ilium has been damaged. It is under the sacrum, and only the anteroventral edge and possibly the posterior iliac blade are observable. Both ischia are present, overlapping one another. The pubes are not preserved.

Ilium: Information from both partial ilia permit a basic interpretation of their morphology. They must have been dorsoventrally high in their anterior region, and from there they appeared to decrease their outline, extending as far as the slender posterior end. We think that the preacetabular region (surface) was larger than the postacetabular region. The acetabulum is proportionately small, recalling the condition in *Archaeopteryx*.

Ischium: The ischia are intimately joined for most of their length, but they are slightly separated in their distal region. The distal prolongation is long, parallel-sided, and without an expansion, quite unlike the condition in *Archaeopteryx*. It has a broad puboischiadic blade, without any indication of an obturator foramen. It is oriented ventroposteriad, perhaps with a small modification relative to its original position.

The few available pelvic elements demonstrate that the ischium of this species has some plesiomorphic features that clearly differentiate it from the peculiar ischium of *Archaeopteryx*. The pubis should have been directed ventrad, perhaps oriented somewhat anteriad, as is suggested by the ventral curvature of the puboischiatic blade.

The pelvic girdle of *Iberomesornis* was probably less derived than that of *Archaeopteryx*, at least insofar as the ischium is concerned.

Femur: Both femora have been preserved in approximately

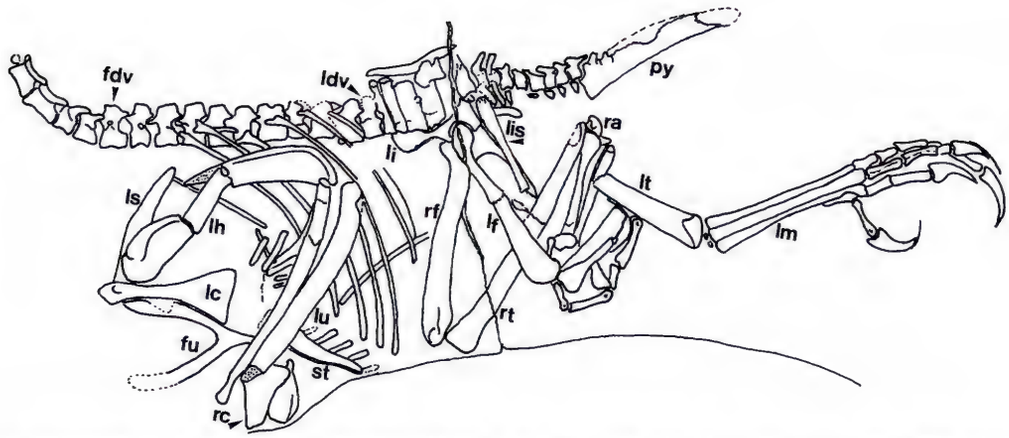

Figure 5. Schematic interpretation of *Iberomesornis romerali* n. gen., n. sp. Abbreviations: **fu,** furcula; **fdv,** first dorsal vertebra; **lc,** left coracoid; **ldv,** last dorsal vertebra; **lf,** left femur; **lh,** left humerus; **li,** left ilium; **lis,** left ischium; **lm,** left metatarsals; **ls,** left scapula; **lt,** left tibia; **lu,** left ulna; **py,** pygostyle; **ra,** right astragalus; **rc,** right coracoid; **rf,** right femur; **rt,** right tibia; **st,** sternum.

their original position. The left femur is broken, and both fragments partially overlap. It is proportionally long, but shorter than the tibia (ratio of 0.78), as in *Archaeopteryx* (0.71–0.77; Wellnhofer, 1974). The relatively small head of the femur projects mediad. Features of the proximal region, such as the major trochanter or iliac facet, are not apparent. The diaphysis is arched slightly forward, especially in the distal half. The distal condyles are moderately developed, and the popliteal depression is visible on the right femur.

There are resemblances to the femur of *Archaeopteryx,* such as in the anterior curvature of the femur (Ostrom, 1976) and in its proportional length to the tibia. The evolutionary level of the *Iberomesornis* femur is evidently not too different from that of *Archaeopteryx.*

Tibia and Fibula: Both tibiae are preserved. The right tibia is almost complete, associated with the astragalus and articulated with the femur and partially exposed in internal view. The left tibia is broken in the middle of the diaphysis. The proximal half, which is articulated to the femur, is exposed laterally, and a fibular fragment is attached to it. The distal half is turned over and exposed in anterior view.

The tibiae are rather straight and somewhat robust. No cnemial crests are apparent. The fibular crest region is covered by the fibular fragment mentioned previously. The anterior side is concave in the distal sector, and the dorsal process of the astragalus fits over it. The lack of tibia–astragalus fusion is, in our opinion, a primitive character shared with *Archaeopteryx* but not with the Ornithurae (Gauthier, 1986; Cracraft, 1986).

The left fibula is very poorly preserved near the left tibia. It does not offer any details for analysis.

Astragalus and Calcaneum: The astragali are situated in their appropriate places, articulated with the foot. Their state of preservation does not reveal any further details about their anatomical features. The right astragalus is exposed on its internal side. It is faintly separated from the right tibia, demonstrating that the two bones were not fused. The left astragalus is exposed on its anterior side. Its relative position shows that it was placed more anteriorly than the left tibia, especially in its distal region.

The anterodorsal process of the astragalus is laminar and broad, as is observable on the left astragalus; in this case, the process tightly overlaps the adjacent tibia. The distal portion of the astragalus is transversely broad, and a large ossification, situated beside the right side of the astragalus, may correspond to the calcaneum, although its position is unexpected.

Two small ossifications above the left metatarsals are preserved; these must be the distal tarsals. The proximal tarsals are separated from the tibiae in *Iberomesornis,* without any evidence of fusion. This condition is similar to that noted for *Archaeopteryx* (Wellnhofer, 1974:198–99, fig. 11). The latter author's remarks, and Ostrom's (1976:121–23) opposite opinion, attracts our attention. The presence of a tibiotarsus in *Archaeopteryx* is defended by Tarsitano (1985). Nevertheless, if we take the general structure of the tarsus and metatarsus of *Archaeopteryx* as a reference, it would seem more likely that the Solnhofen bird's tarsus represents a condition similar to that of *Iberomesornis,* coinciding with the metatarsals in its lack of fusion.

Metatarsals and Phalanges: The metatarsals of both sides are preserved. The left metatarsals are exposed in anterior view, well articulated among themselves, and with the digits. The right metatarsals are rather too obscure to be interpreted accurately, but they are also associated with digits. There are no traces of fusion between any of the metatarsals, and we can observe that they are pneumatic.

The left metatarsals are broadly exposed in anterior view, without any marked indications of hypertrophy or reduction. They are subequal. Metatarsal III is slightly more developed, not only in thickness but also in length. Metatarsal II is similar to metatarsal IV in being noticeably more slender. Metatarsal I is visible only distally and has been moved from its original position. It is curved distally, and it articulates with two reverted phalanges. One of the latter, the ungual, is dorsoventrally deep and of large size. Metatarsal II articulates to three phalanges; the first one is rather short, the second one is enlarged, and the ungual is similar to that of digit I in size and shape.

Metatarsal III is straight, with a small lateral expansion of the proximal region. It is the longest of the four and is articulated to four phalanges. The proximal phalanges are long, the third is much shorter, and the ungual is slightly smaller than the unguals of digits I and II, although dorsoventrally deep. Metatarsal IV is thinner distally than metatarsals II and III, and it is articulated to five phalanges; the three proximal ones are rather short and the fourth is elongated. The ungual is long and less curved, a little more slender than the rest. Preserved sheaths are observed in almost all ungual phalanges. They follow the phalangeal direction and they could be the corneous claws. The phalangeal formula of *Iberomesornis* is 2–3–4–5.

Table 1. Characters × taxa matrix.

	Cervical neurapophyses	Dorsal neural arches	Cervical ribs	Cervicodorsal hypapophyses	Dorsal vertebrae	Sacral vertebrae	Sacral vertebrae hypapophyses	Pygostyle	Caudal vertebrae zygapophyses	Uncinate processes	Gastralia	Coracoid	Furcula	Humerus/ulna length	Pelvis fusion	Ilium-ischium-pubis	Tarsals	Metatarsals	Reverted hallux
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Coelurosaurs and Deinonychosaurs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Archaeopteryx	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Iberomesornis	1	1	1	0	1	0	1	1	0	0	1	1	1	1	0	0	0	0	1
Ornithurae	1	0	1	1	2	1	0	1	1	1	1	1	1	1	1	1	1	1	1

DISCUSSION

INTRODUCTION

Iberomesornis romerali represents, as a whole, a derived morphology that is intermediate between *Archaeopteryx* and later birds (Ornithurae *sensu* Cracraft, 1986). It shares a large number of apomorphies with the latter, particularly in the shoulder girdle, anterior limbs, and pygostyle. It also shares some symplesiomorphies held in common with *Archaeopteryx*, Coelurosauria, and Deinonychosauria, primarily in the sacrum and hindlimb. It also shares some characters of the pelvis with *Archaeopteryx*, which has some derived features of the ischium (Ostrom, 1976; Wellnhofer, 1985).

Following other authors (Ostrom, 1976; Gauthier, 1986; Cracraft, 1986), we have chosen the theropod groups Coelurosauria and Deinonychosauria as outgroups for character polarity determination.

CHARACTER ANALYSIS (SEE TABLE 1)

1. Reduced cervical neurapophyses. *Iberomesornis* does not have developed neural spines on the cervical vertebrae. This is a derived character shared with the Ornithurae. The primitive condition (presence of well-developed neurapophyses) is obviously present in forms such as *Compsognathus* and *Deinonychus*, and it persists in *Archaeopteryx*.

2. High dorsal neural arches. In *Iberomesornis* the neural pedicles are high, becoming narrow in the subzygapophyseal region. In *Archaeopteryx* and in theropods such as *Compsognathus* and *Deinonychus*, the dorsal neural arches are relatively low, with a small space between the zygapophyses and the vertebral centra, which represents the primitive condition. We consider this character as an autapomorphy of *Iberomesornis*.

3. Fused cervical ribs. There are indications that the posterior cervical ribs of *Iberomesornis* were fused to the vertebral centrum. We think that this is a synapomorphy shared with the Ornithurae. *Archaeopteryx* and other theropods have free cervical ribs.

4. Cervicodorsal hypapophyses. This is an ornithurine synapomorphy that is lacking in *Iberomesornis*, *Archaeopteryx*, and theropods.

5. Number of dorsal vertebrae. There are 4–6 dorsal vertebrae in modern birds (Van Tyne and Berger, 1976) and 13–14 in *Archaeopteryx*. We note an intermediate number of 11 in *Iberomesornis*. This represents an apomorphy relative to *Archaeopteryx* and theropods.

6. Number of sacral vertebrae. This is high in modern birds, ranging from 10 to 23, because of the incorporation of dorsal and caudal vertebrae into a broad synsacrum. The sacrals are five in number in *Archaeopteryx* (Ostrom, 1976), coinciding with the number in *Iberomesornis*.

7. Hypapophyses in sacral vertebrae. The presence of this feature is apomorphic for *Iberomesornis*, and it may be related to sacral region reinforcement. Sacral hypapophyses are lacking in the Ornithurae and in *Archaeopteryx*.

8. Free caudal vertebrae and pygostyle. The presence of free caudal vertebrae in association with a pygostyle is a derived character relative to the condition in *Archaeopteryx*. This character is shared with the Ornithurae.

9. Free caudal vertebrae zygapophyses. The ornithurae are characterized by the absence of zygapophyses in the caudal vertebrae (Gauthier, 1986). *Iberomesornis* has functional zygapophyses, at least in the last caudal segments, a symplesiomorphy shared with *Archaeopteryx* and theropods.

10. Uncinate processes on the ribs. Uncinate processes are a synapomorphy of the Ornithurae that are not present in *Iberomesornis* or in *Archaeopteryx*.

11. Absent or reduced gastralia. The presence of gastralia is a plesiomorphic character present in primitive Archosauria and even in *Archaeopteryx*. They were not seen in *Iberomesornis*. If sternal development was related to the disappearance of gastralia, it is likely that the latter were extremely reduced or already absent in *Iberomesornis*.

12. Distally expanded coracoid. Coracoid structure in *Iberomesornis* is highly derived, with a broad expansion for contact with the sternum and a well-developed coracoid head. The coracoid morphotype of *Iberomesornis* represents a derived condition relative to that in *Archaeopteryx* and a synapomorphy shared with the Ornithurae.

13. Furcula. Some theropods (Barsbold, 1983) and *Archaeopteryx* have a furcula without a developed hypocleidium and a broad clavicular angle (about 90°), which is the primitive con-

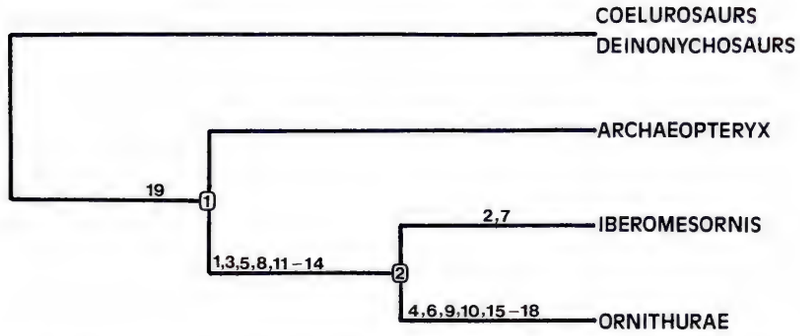

Figure 6. Cladogram based on characters × taxa matrix of Table 1. See text for identification of characters.

dition. *Iberomesornis* has a conspicuous styloid furcular process, similar to that of many Ornithurae, and a lower clavicular angle (60°).

14. Humerus/ulna length. Ulnar length exceeds humeral length by about 10 percent in *Iberomesornis*. This derived state is found in most Ornithurae, but the ratio is just the reverse in the Theropoda and *Archaeopteryx*.

15. Fused pelvis. Pelvic elements are unfused in theropods, *Archaeopteryx*, and *Iberomesornis* and fused in Ornithurae.

16. Ilium-ischium-pubis not parallel posteriorly (Cracraft, 1986). This primitive character is present in *Archaeopteryx* and *Iberomesornis*. The Ornithurae have a more or less parallel disposition of pelvic elements.

17. Unfused tarsals. In *Iberomesornis*, the astragalus, the probable calcaneum, and both distal tarsals are fused neither among themselves, nor with the tibia, nor with the metatarsals. This represents a primitive level of organization of the posterior limb, similar to that attained in theropods and *Archaeopteryx*.

18. Unfused metatarsals. The metatarsals of *Iberomesornis* show no trace of fusion, sharing this feature with *Archaeopteryx*. The plesiomorphic nature of this condition relative to that in Ornithurae is obvious. If, as suggested by some authors, *Archaeopteryx* has some degree of fusion, then it is necessary to postulate a parallelism for this feature in *Iberomesornis* (Cracraft, 1988).

19. Reverted hallux. *Archaeopteryx*, *Iberomesornis*, and the Ornithurae show true reverted first digits in the pes (Tarsitano, 1985). Theropods have only a partial reversion.

PHYLOGENETIC ANALYSIS

The results of the phylogenetic analysis presented in a cladogram (Fig. 6) show *Iberomesornis* to be the sister-group of the Ornithurae. We see here a clade (node 2) supported and defined by eight derived characters: reduced cervical neurapophyses, fused cervical ribs, reduced number of dorsal vertebrae, presence of a pygostyle, gastralia absent, strut-like coracoid, furcula with a developed hypocleidium and low clavicular angle, and ulna longer than humerus.

On the other hand, *Iberomesornis* is characterized by two autapomorphies: the presence of relatively high dorsal neural arches and the existence of sacral hypapophyses. *Archaeopteryx* is the sister-group of the Ornithurae + *Iberomesornis*. This node (1) is defined in our analysis by a true reversed hallux. Most authors define this node by the presence of feathers (Padian, 1985) or other osteological characters (Martin, 1987; Cracraft, 1986). Although the presence of feathers in *Iberomesornis* is very probable (see Introduction), no direct evidence indicates their former existence in this bird.

SYSTEMATIC DISCUSSION

Iberomesornis romerali represents a hitherto unknown stage of avian evolution, and we recognize that the correct systematic interpretation of it will require a broader knowledge of its anatomy and must be the result of further critical discussions. Nevertheless, the primitive and derived skeletal features that this species presents clearly show that we are dealing with a new higher taxon.

Iberomesornis romerali differs from the Archeornithes by having the noticeably derived characters, already noted, in its shoulder girdle, cervical vertebrae, and pygostyle. Its inclusion in the Ornithurae would not be admissible given the obvious plesiomorphies in its sacrum, pelvis, and hindlimb, especially in the tarsus and metatarsus. The reverted hallux, however, contradicts this assessment. Thus, *I. romerali* cannot fit into existing classification schemes, and it may eventually require the recognition of a supraordinal taxon similar in rank to the Ornithurae.

CONCLUSIONS

We summarize the conclusions suggested by this new specimen as follows.

1. *Iberomesornis romerali* represents an intermediate organizational level between *Archaeopteryx* and later birds, in which the definitive active flight structures are already developed. *Iberomesornis* is the closest known sister-group of the Ornithurae.

2. From the *Archaeopteryx* evolutionary grade onward, avian evolution was concentrated first in the pectoral region. The pelvis and hindlimb were delayed as regards transformation rate. Therefore, we have a case of differential evolutionary rates. The small size of *Iberomesornis* is consistent with this evolutionary trend, active flight being easier for a small tetrapod.

3. The distribution of some characters in the phylogenetic hypotheses proposed for the early birds (Martin, 1984; Cracraft, 1986) must be revised, because the presence of a strut-like coracoid found in *Iberomesornis* has previously been considered to be a synapomorphy of carinate birds.

4. The specialized hallux of *Iberomesornis* suggests an adaptation to the final flight stage, in order to have a firm grasp when perching. If this were the case, it would be the posterior limb's most remarkable derived feature, related to flight and shared by *Archaeopteryx*.

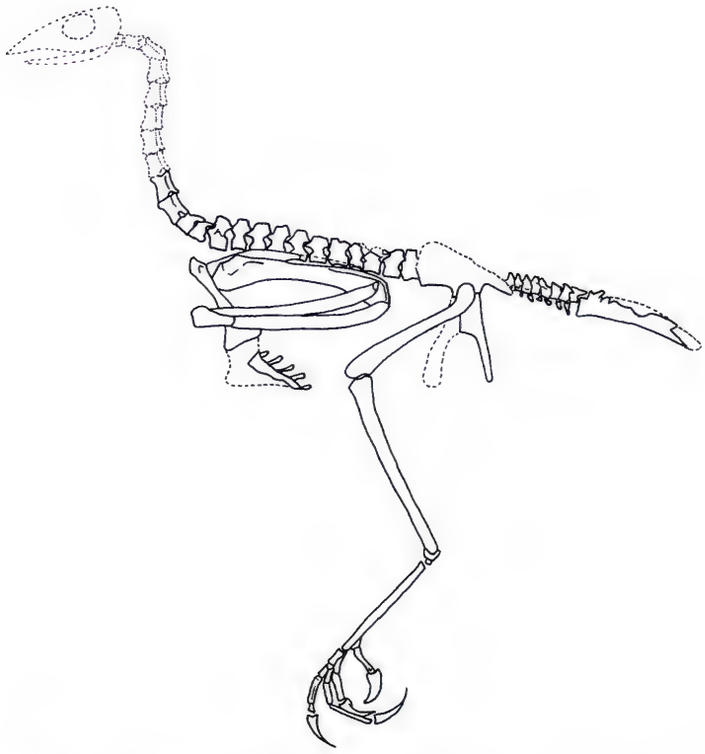

Figure 7. Schematic reconstruction of the skeleton of *Iberomesornis romerali* n. gen., n. sp.

5. Neural spine reduction and the development of the osseous flange linking the lateral zygapophyses should have taken place in the cervical vertebrae before the appearance of heterocoely.

6. As *Iberomesornis* suggests, the reduction in the number of dorsal vertebrae presented by modern birds should have happened after development of osseous structures in the pectoral region appropriate for the later type of active flight.

7. The features of the pygostyle and the presence of free caudal vertebrae in *Iberomesornis* suggest that reduction of caudal vertebrae should have taken place by progressive fusion from the end forward, with simultaneous reduction of the posterior region of the pygostyle.

8. If *Archaeopteryx* is the ancestral type, development of a pygostyle and pectoral girdle characteristic of modern birds would have happened between the Early Tithonian (some 150–145 mya) and the Hauterivian (some 130–125 mya), being an example of tachytelic evolution.

9. It is very likely that *Iberomesornis,* intermediate between *Archaeopteryx* and the Ornithurae, represents a northern hemisphere Cretaceous faunal element. Meanwhile, the Enantiornithes (Walker, 1981), found in the Australian Lower Cretaceous, the Argentinean Upper Cretaceous with several not yet determined taxa and in the Upper Cretaceous of the USA (Brett-Surman and Paul, 1985), represents a Cretaceous vicar that evolved in isolation (Bonaparte, 1986) from common ancestors with pangeic distribution.

RECONSTRUCTION OF *IBEROMESORNIS*

Based on the analysis of the skeleton of *Iberomesornis* (Fig. 7), a life reconstruction is proposed (Fig. 8). The foreneck region and head are, of course, hypothetical. The presence of teeth in

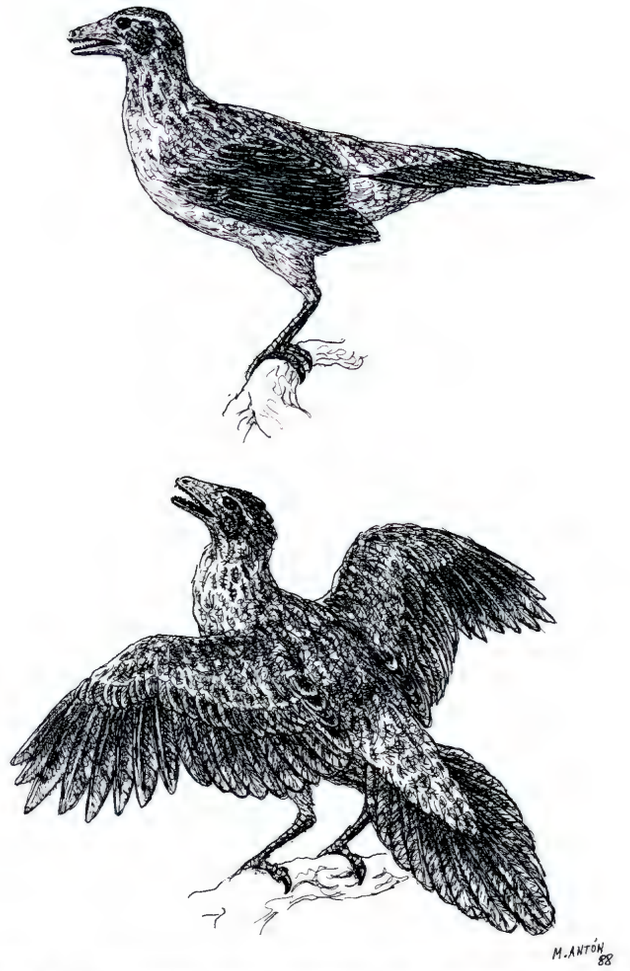

Figure 8. Life reconstruction of *Iberomesornis romerali* n. gen., n. sp.

Iberomesornis is consistent with the phylogenetic position suggested here. The feather pattern is based on *Archaeopteryx.*

ACKNOWLEDGMENTS

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A NEW FLIGHTLESS LANDBIRD FROM THE CRETACEOUS OF PATAGONIA

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ABSTRACT. A new fossil bird is described from the Upper Cretaceous (Coniacian) of Patagonia (Neuquén, Argentina), based on an incomplete, articulated skeleton and associated fragments plus an almost complete individual enclosed in sandstone and not yet prepared. This bird is named *Patagopteryx deferrariisi* new genus, new species, and it is referred to a new family, Patagopterygidae, and a new order, Patagopterygiformes. *Patagopteryx deferrariisi* was a terrestrial bird, the size of a domestic fowl, with robust legs and wings too small for flight.

Key words: Aves, ratites, Cretaceous, Patagonia, fossil bird.

INTRODUCTION

We present here a contribution to the knowledge of Mesozoic birds, based on excellent material from Neuquén Province, Argentina, for which we propose a new genus and species in its own new family and order.

At present, fewer than 30 genera of Cretaceous birds are known (Elzanowski, 1983), most of which are aquatic and almost all of which are from the Northern Hemisphere (Laurasia).

The Enantiornithes (Walker, 1981) were the first known group of birds reported from the continental Cretaceous of Gondwana (Maastrichtian, Argentina). These birds introduced new ideas regarding osteological features of birds and consequently provided an important advance in the study of evolution in the Class Aves. New information from a previously unknown group of birds from the continental Cretaceous (Coniacian) of Gondwana may now further our understanding of the evolution of birds in the Southern Hemisphere.

The materials described herein include an incomplete, articulated skeleton, deposited at the Museo Argentino de Ciencias Naturales, Neuquén Collection (holotype, MACN-N 03), and several associated pieces of tarsometatarsi and phalanges (MACN-N 10) of another individual, all from the same 1984 collection. There is also a skeleton that may be complete (MACN-N 11), collected at the type locality (Fig. 1) in 1985, that is still enclosed in sandstone. This last specimen provides some important details reported briefly in this work. All of this material was collected by personnel of the Universidad Nacional del Comahue, Neuquén, Neuquén Province, Argentina.

The associated fauna indicates that the habitat frequented by the Cretaceous birds described herein was a fluvial plain. Crocodilians (*Notosuchus* Woodward 1896 and genus indeterminate), snakes of the family Dinilysidae, small theropod dinosaurs, and indeterminate lacertilians have been reported from the same beds.

SYSTEMATICS

Order Patagopterygiformes new order

DIAGNOSIS. Terrestrial birds with reduced wings. Cervical vertebrae heterocoelous. Thoracic vertebrae procoelous, not ankylosed, without formation of notarium. Ilium weakly fused to synsacrum, with the pars preacetabularis in vertical position and far from the long axis of the synsacrum; pars postacetabularis is wide and robust, giving rise to two massive posterior apophyses. Iliac crest single and continuous to the posterior portion of the ilium. Ischium and pubis slanted backward, enclosing two posterior notches (open ilio-ischiatic fenestrae). Synsacrum dorsoventrally compressed and transversely wide (the opposite of the condition in Enantiornithes), with anterior articular surface strongly procoelous. Humerus without pneumatic foramen. Tibiotarsus with outer cnemial crest anteriorly developed; tendinal groove without supratendinal bridge.

Family Patagopterygidae new family

DIAGNOSIS. As for order.

Genus *Patagopteryx* new genus

TYPE SPECIES. *Patagopteryx deferrariisi* new species.
DIAGNOSIS. As for order.
ETYMOLOGY. *Patagon,* Spanish, in reference to Patagonia, the region of Argentina where the fossils were collected, meaning "big foot," a term once applied to the Amerindian inhabitants of the area; *pteryx,* Greek, wing; feminine.

Patagopteryx deferrariisi new species

Figures 2–19

HOLOTYPE. Incomplete postcranial skeleton, consisting of 5 cervical vertebrae, 11 thoracic vertebrae, the synsacrum, 2 caudal vertebrae, and much of the pectoral and pelvic girdles, wings, and hindlimbs (Figs. 2–11, 14–17). Museo Argentino de Ciencias Naturales MACN-N 03.

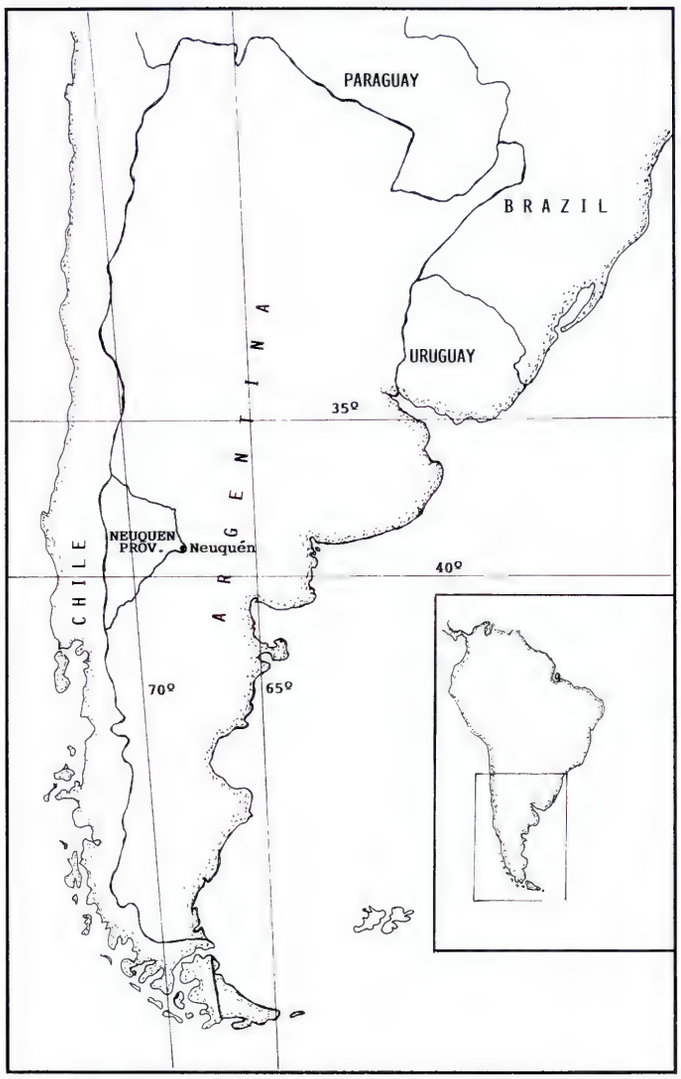

Figure 1. Map showing the type locality of Neuquén, Neuquén Province, Argentina.

PARATYPES. MACN-N 10, two distal ends of tarsometatarsi, phalanges, and indeterminate fragmentary bones; MACN-N 11, a nearly complete, articulated specimen, not yet prepared.

DIAGNOSIS. As for order.

TYPE SECTION AND HORIZON. From the lower section of the Rio Colorado Formation, Neuquén Group, Upper Cretaceous (Coniacian) (Legarreta and Gulisano, 1989). The holotype was collected 200 m east of the buildings of the Universidad Nacional del Comahue, Neuquén, Neuquén Province, Argentina (Fig. 1).

ETYMOLOGY. The specific name is in homage to Professor Oscar de Ferrariis, Director, Museo de Ciencias Naturales, Universidad Nacional del Comahue, who was responsible for the collection of the specimens described herein.

DESCRIPTION. The osteological nomenclature followed is that of Howard (1929) and, in some cases, that adopted by Baumel (1979).

Cervical Vertebrae. Only the last five cervicals are preserved, and they are heterocoelous. The centrum is approximately quadrangular in cross-section, with the middle portion narrowest; the ventral face is almost flat with angled lateral edges. The last cervical resembles the thoracics that follow in having a small hypapophysis. The general morphology and proportions of the cervicals resemble those of Recent species of the family Tinamidae (Figs. 3–5). Measurements (mm) of the length of the ventral face of the cervical centra of MACN-N 03, in cranial–caudal order: 17.5, 16.5, 16.0, 14.8, 13.2.

Thoracic Vertebrae. Eleven thoracic vertebrae are present, including the last two or three that were articulated with the ilium. The fovea costalis is strongly pointed and the vertebrae are procoelous. The three anterior thoracic vertebrae show a transition to the heterocoelous cervicals. The six anterior thoracics each have a pronounced crista ventralis on the centrum, without, however, the formation of a notarium. The centra of the five posterior thoracic vertebrae are dorsoventrally flattened and transversely wide, leading to the configuration in the synsacrum. The neural spines are flattened and quadrangular in shape in lateral view; there is neither fusion nor contact between them (Figs. 2–4, 6, 7). Measurements (mm) of the length of the ventral face of the thoracic centra of MACN-N 03: 1st, 10.4; 2nd, 10.3; 3rd, 9.8; 4th, 10.5; 5th, 12.0; 6th, 11.5; 7th, 11.8; 8th, 12.0; 9th, 11.8; 10th, 9.4; 11th, 10.1.

Synsacrum. Formed by nine vertebrae, with the anterior articular surface strongly procoelous; a slight dorsal arch (kyphosis); sulcus ventralis very ample, occupying more than the anterior half. The last two synsacral vertebrae do not articulate with the ilium (Figs. 2–4, 6, 7). Measurements (mm) of the synsacrum of MACN-N 03: total length, 53; greatest width, 14 (at the anterior ⅓).

Caudal Vertebrae. Two caudal vertebrae from the holotype do not join directly to the terminal portion of the synsacrum, nor to each other, indicating that some of the first caudal vertebrae are missing. In specimen MACN-N 11, there are indications of a reasonably developed caudal region, more developed than in Recent birds, without a pygostyle.

Scapula. The proximal portions of both scapulae of the holotype were preserved. The acromial process and glenoid are quite well developed. There is no scapulocoracoid fusion, and the articular surface is convex; the neck portion is laminar (Fig. 8). Maximum width: 16 mm.

Coracoid. Only the sternal portion of the right coracoid was preserved (Fig. 6). The convex posterior face has a triangular depression (sternocoracoidal fossa), resembling that in the Enantiornithes.

Clavicle. We tentatively identify two pieces of the holotype as the proximal ends of the clavicles (Fig. 8D, E).

Humerus. The humerus is of reduced proportions, its length corresponding to 65 percent of that of the femur and 46 percent of that of the tibiotarsus. No pneumatic foramen is present. The bicipital crest projects anteriad, delimiting an extensive bicipital furrow; diaphysis arched anteriad, mainly in the proximal half; external condyle appears to have been oriented parallel to the long axis of the diaphysis (the opposite of the condition in Enantiornithes and *Alexornis* Brodkorb 1976, where the external condyle is oriented transversely to the long axis of the diaphysis). The entepicondyle is produced mediad, not distad as in the Enantiornithes and *Alexornis* (Figs. 9–12). Measurements (mm) of the left humerus of MACN-N 03: total length, 65.4; proximal width, 17.2; distal width, 17.4.

Ulna. The proximal end of the left ulna and radius were articulated to the corresponding humerus in the holotype. The portion of ulna preserved is 16.8 mm long and 12.0 mm in maximum width. It is very compressed laterally, and the external cotyla is very spread, joining with the head of the radius. The bicipital attachment is very prominent (Fig. 9).

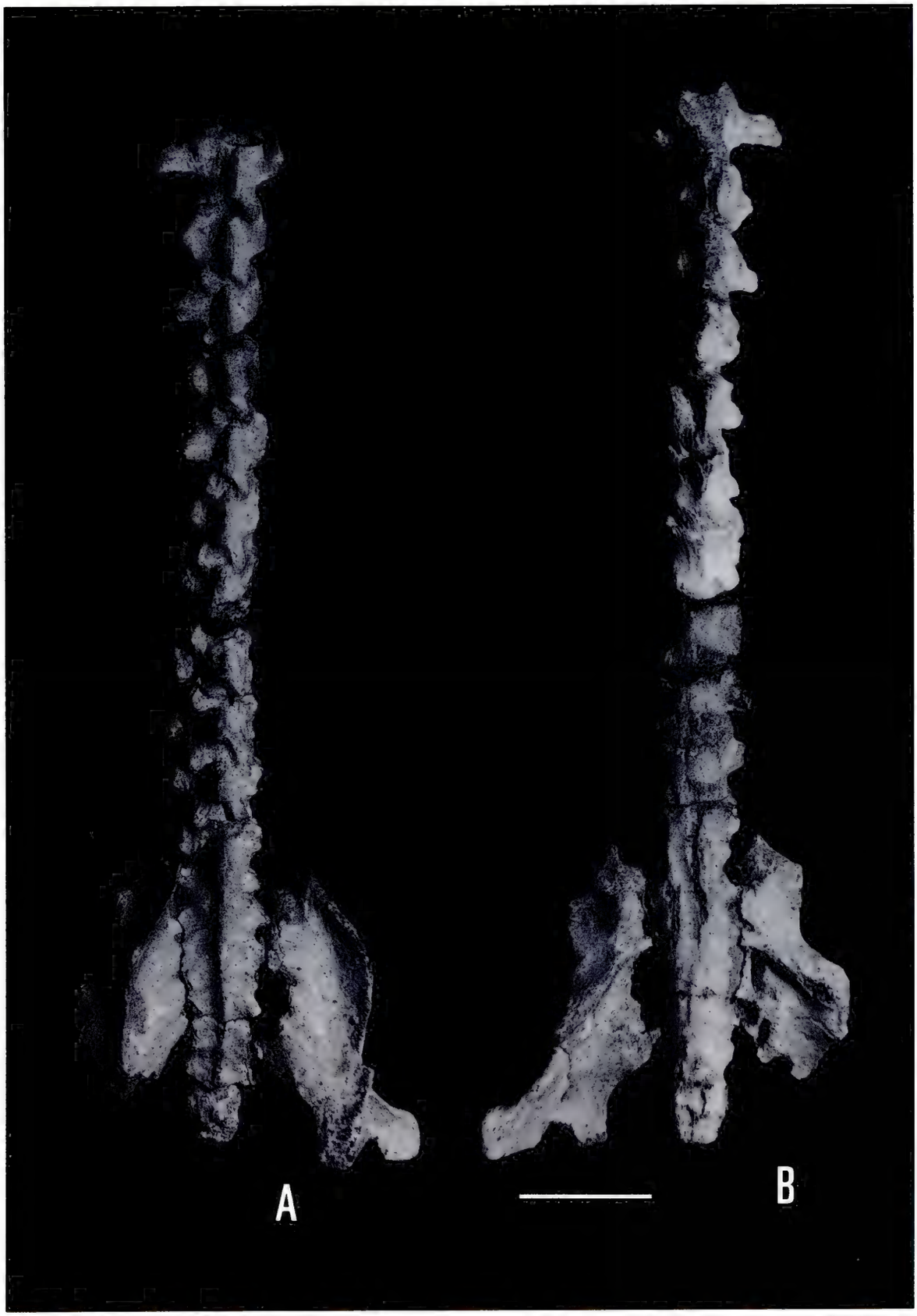

Figure 2. Thoracic vertebrae (from the second posteriad), synsacrum, and ilium of *Patagopteryx deferrariisi* n. gen., n. sp. (holotype, MACN-N 03): dorsal (**A**) and ventral (**B**) views. Scale bar = 2 cm.

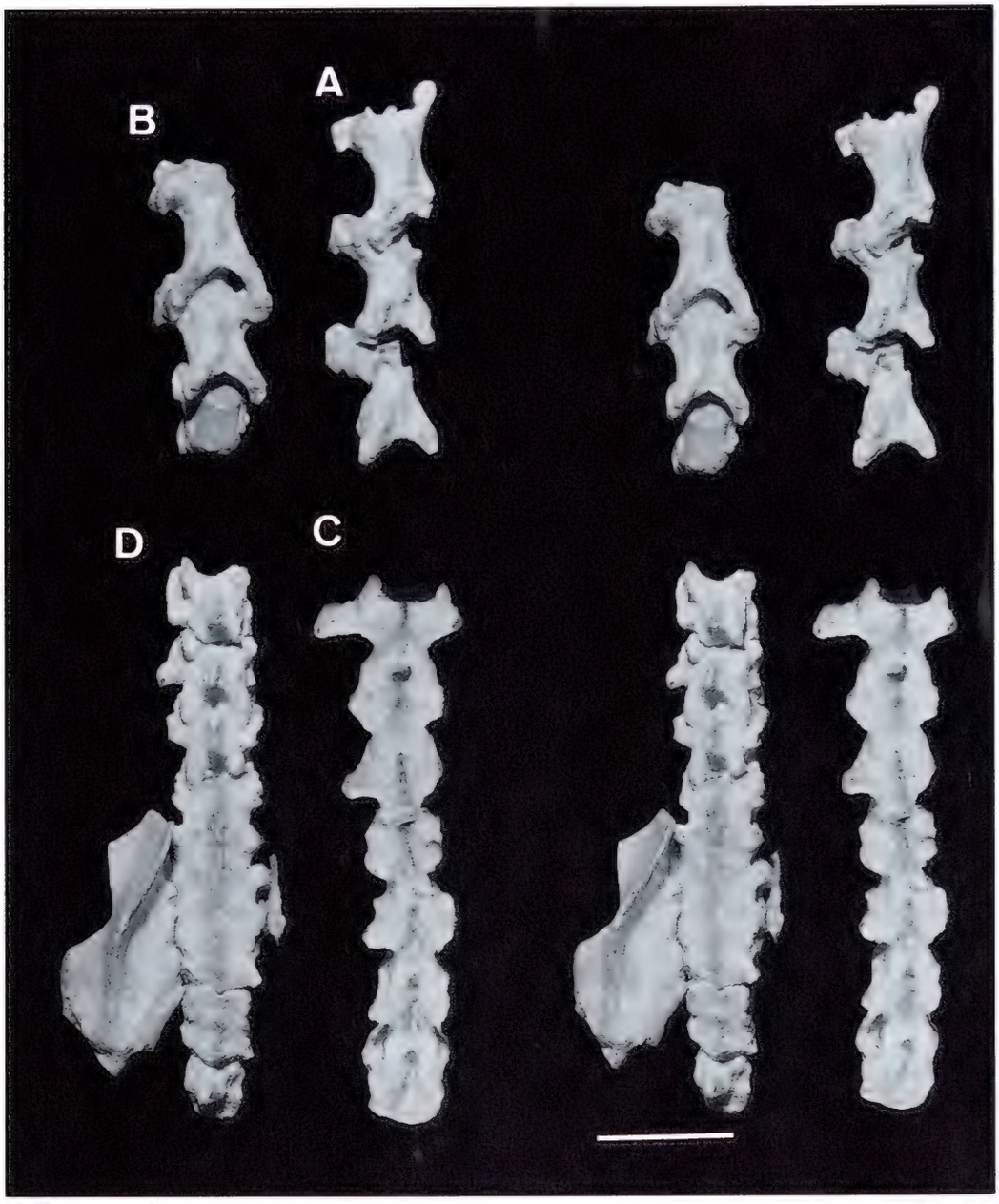

Figure 3. Stereophotographs of *Patagopteryx deferrariisi* n. gen., n. sp. (holotype, MACN-N 03): the last five cervical vertebrae (**A, B**), all thoracic vertebrae (**C, D**), the synsacrum, and the left ilium (**D**); dorsal view. Scale bar = 2 cm.

Radius. The proximal portion of the left radius is 9 mm long. It does not show any osteological characters (Fig. 9). In MACN-N 11, the estimated total length of the ulna and radius is 53 mm.

Ilium. The pars preacetabularis is characterized by a high, vertical ridge at a distance from the long axis of the synsacrum. The superior edge of the ridge is the beginning of the iliac crest (present only in MACN-N 11). The pars postacetabularis, almost complete on the right side of the holotype (Figs. 2, 7, 13) is robust and terminates by giving rise to two massive posterior processes, one medial and another lateral. The lateral one is stronger, indicating a solid muscular insertion. The anterior and posterior iliac crests are continuous, forming a single crest that is very prominent dorsally and extends from the more anterior portion to the posteromedial process. The antitrochanter is very large. Total length of the holotype right ilium is 68.4 mm.

Ischium and Pubis. Both are absent in the holotype but evident in specimen MACN-N 11, where they are inclined obliquely posteroventrad, forming the large ilio-ischiatic and ischiopubic notches, in a manner that resembles that typical of ratites. The ischium becomes more laminar posteriorly, descending to a horizontal position and approaching the medial plane in a way that is similar to that seen in *Rhea* Brisson 1760 (Fig. 13).

Femur. Robust, forward arched with the lineas intermuscularis prominent (Figs. 14, 15). The length is about 73 percent of that of the tibiotarsus. The crista trochanteris is robust and projects forward, forming a deep fossa trochanteris; the lateral

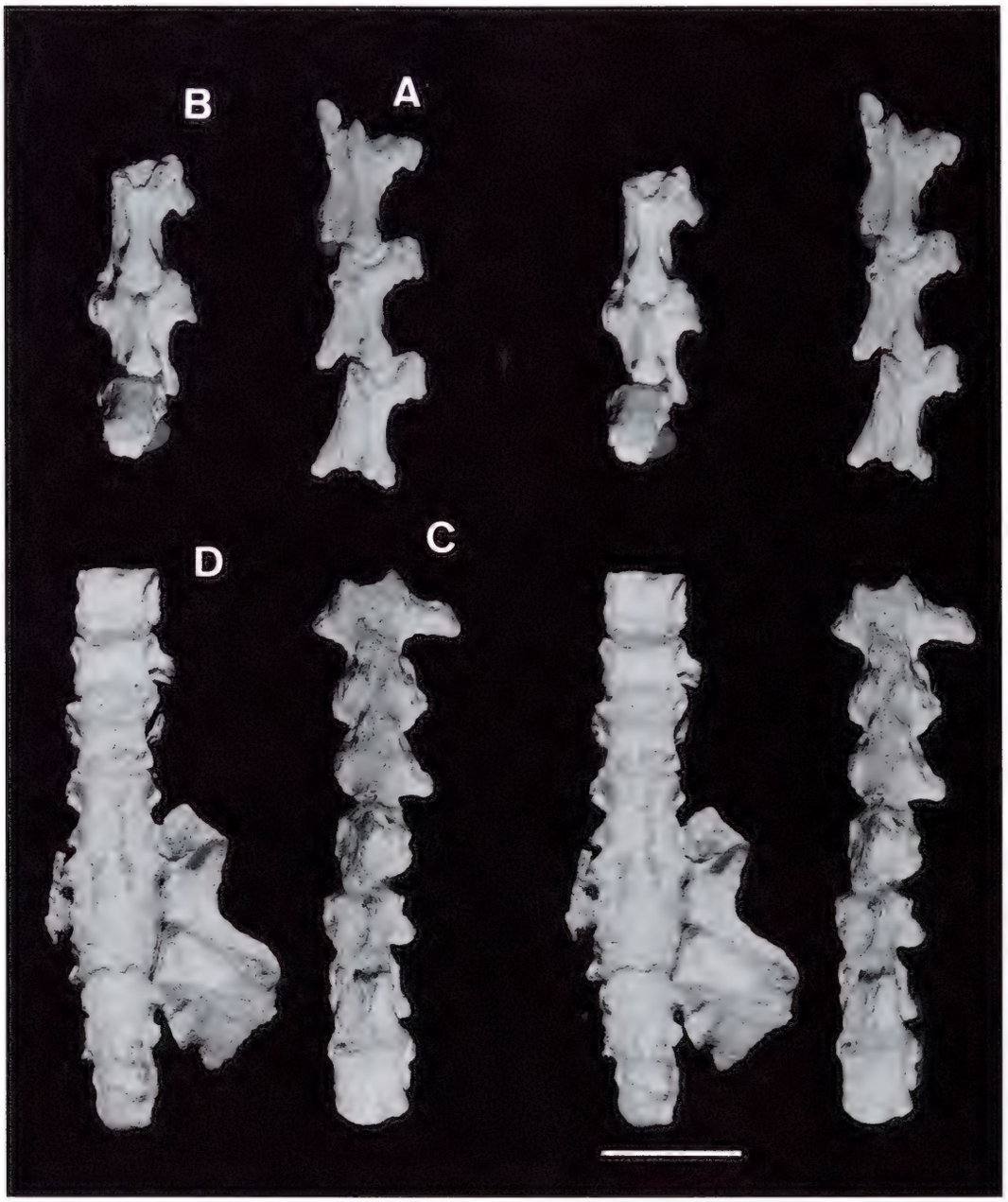

Figure 4. Stereophotographs of *Patagopteryx deferrariisi* n. gen., n. sp. (holotype, MACN-N 03): the last five cervical (**A, B**) vertebrae, all thoracic vertebrae (**C, D**), the synsacrum and the left ilium (**D**); ventral view. Scale bar = 2 cm.

portion of the trochanter gives rise to a wide planar surface similar to that in Recent ratites; and the fossa poplitea is deep and triangular in form. The condylae are not preserved. Measurements (mm) of the holotype femora: left, total length (straight line), 98 as preserved (estimated to be 103 mm if complete distally); right, axis of femoral neck, 20 mm; midshaft transverse diameter, 10.4; midshaft anteroposterior diameter, 11.8.

Tibiotarsus. The outer cnemial crest is anteriorly developed (Fig. 16D), as in rheas, ostriches, and *Diogenornis* Alvarenga 1983. The fibular crest is prominent, extending distad about 40 percent of the diaphysis. The external condyle is rounded, with the anterior part turning proximad to meet the shaft at a small angle. The tendinal groove is in a very medial position, without a supratendinal bridge (Figs. 16, 17). In specimen MACN-N 11, the incisura intercondylaris is wide and shallow, as in ratite birds. Total length of the left tibiotarsus as preserved is 134 mm (estimated to be 140 mm if complete).

Tarsometatarsus. A proximal end of the right(?) tarsometatarsus of the holotype shows that the intercotylaris prominence and hypotarsus are practically absent (Figs. 16E, F, 18). The distal portion of the holotype shows that the trochleae are very short, with the middle one being larger, more robust, and wider than the other two (Figs. 16, 18). In specimen MACN-N 11, the tarsometatarsus is very flattened anterioposteriorly, and the posterior surface is planar and slightly concave proximally. Measurements (mm) of the proximal end: width, 17.1; depth, 12.7.

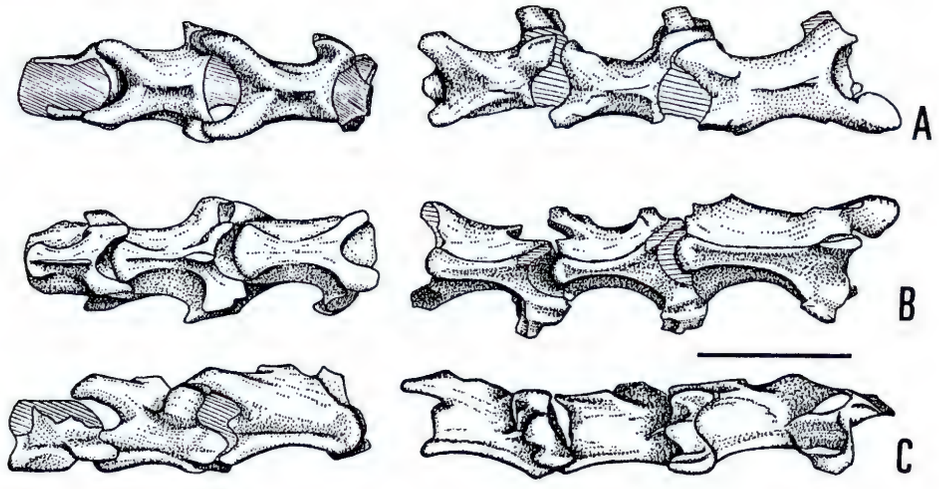

Figure 5. The last five cervical vertebrae and the first thoracic vertebra of *Patagopteryx deferrariisi* n. gen., n. sp. (holotype, MACN-N 03), in dorsal (**A**), ventral (**B**), and lateral (**C**) views. Scale bar = 2 cm.

The estimated total length of the tarsometarsus is 52 mm, or about 35 percent of that of the tibiotarsus (Fig. 16H).

Phalanges. Some phalanges were preserved with the holotype, as well as part of MACN-N 10. They have a high, narrow aspect. The proximal phalanx of digit III is the longest at 19 mm. The total length of digit III, including the ungual (specimen MACN-N 11) is 57 mm, or greater than the tarsometatarsus. The hallux is present but apparently nonfunctional (Figs. 16H, 19).

From specimen MACN-N 11, still being prepared, we can anticipate some additional features: a small skull, with a prominent frontoparietal suture, and a wide, flat sternum, probably without carina (medial portion not preserved).

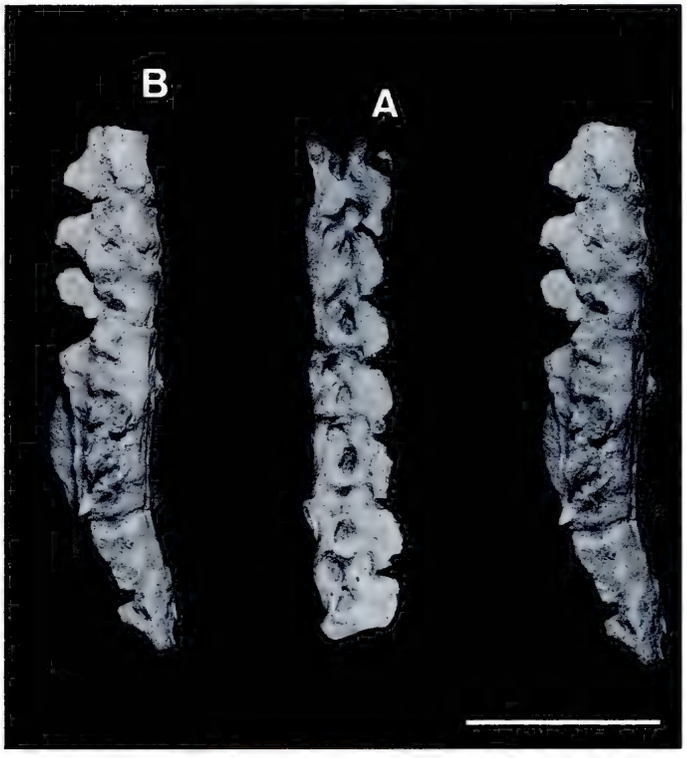

Figure 6. *Patagopteryx deferrariisi* n. gen., n. sp. (holotype, MACN-N 03). **A.** Thoracic vertebrae, from 2nd to 8th, in left side view. **B.** Stereophotographs of the last thoracic vertebrae, from 9th to 11th, and the synsacrum, in right lateral view. Scale bar = 2 cm.

COMPARISONS WITH OTHER MESOZOIC BIRDS

Among Mesozoic birds represented by a good portion of the skeleton, the Enantiornithes, *Gobipteryx* Elzanowski 1974, and *Alexornis* Brodkorb 1976 are classified along with *Archaeopteryx* in the subclass Sauriurae by Martin (1983, 1984). They are all flying birds, with developed wings, long humeri with deltoid crests expanded laterally, and the external condyles placed transversely to the diaphysial axis. *Patagopteryx* differs in all these features, having robust hindlimbs and reduced wings that are not appropriate for flight, and it does not correspond to the Sauriurae in features of the shoulder girdle or tarsometatarsus, which is unfused distally in the Sauriurae.

Compared with birds of the subclass Ornithurae from the Mesozoic, *Ichthyornis* has well-developed wings and small hindlimbs, exactly the opposite from *Patagopteryx*. The morphology of the limbbones in the subclass Ornithurae is very distinctive, and the vertebrae of *Ichthyornis* are also different in that they resemble those of terns (Marsh, 1880). The hesperornithiforms were highly adapted to aquatic life, having the pelvis extremely elongated and a very slim, long, and fragile humerus. The morphology of the femur and tibiotarus is very different from that of *Patagopteryx* (Fig. 12). Both *Hesperornis* and *Patagopteryx* have the ilio-ischiatic and ilio-pubic fenestrae open.

Another Early Cretaceous (Neocomian) bird, from Mongolia, is *Ambiortus dementjevi* Kurochkin 1982, which, according to Olson (1985:87), "... was unquestionably a true volant bird .... It may also share some similarities with *Ichthyornis*, particularly in the humerus." Also, the vertebrae of *Ambiortus* appear to be amphicoelous, as in *Ichthyornis*, and the same arguments for those birds pertain here.

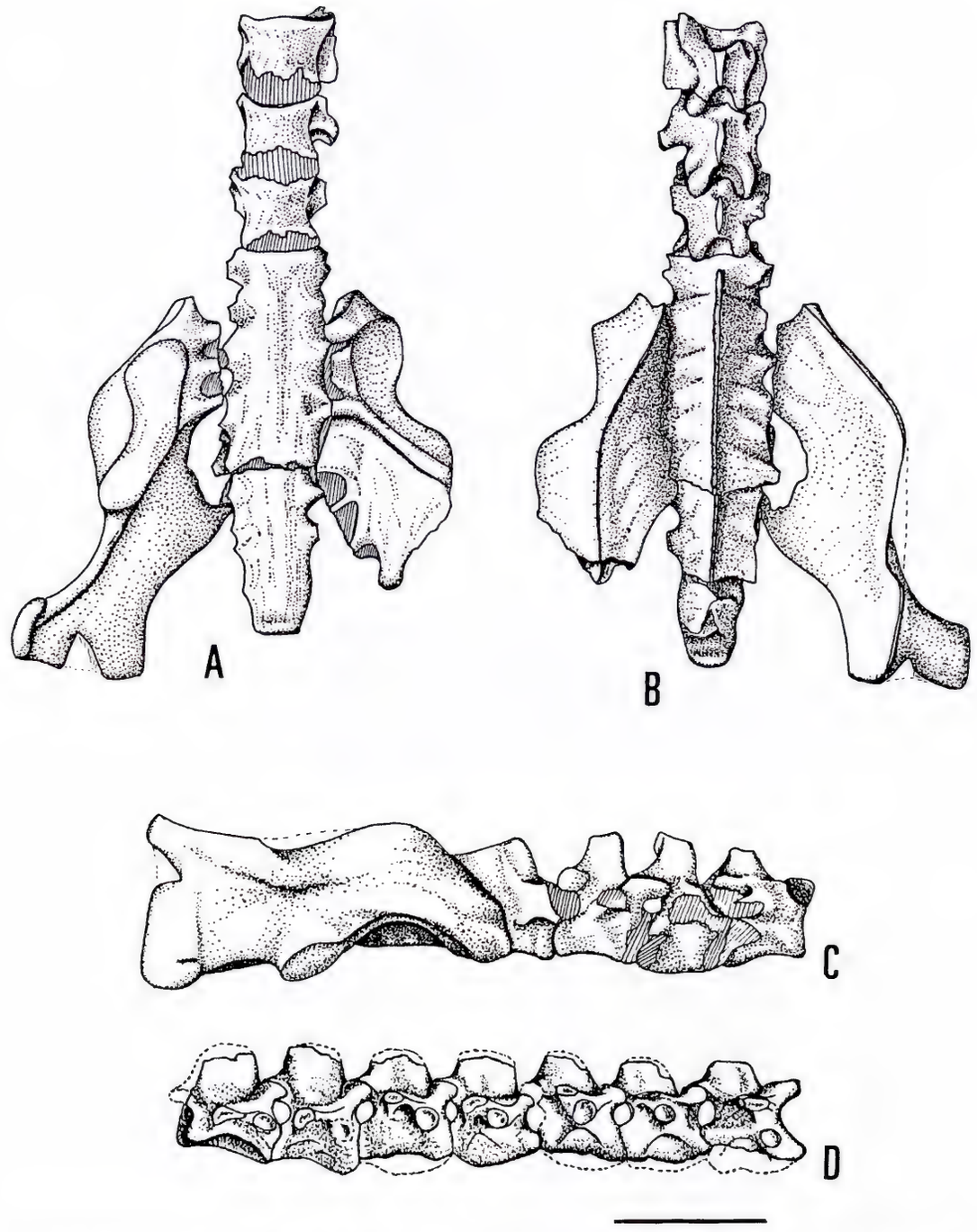

Figure 7. Pelvis of *Patagopteryx deferrariisi* n. gen., n. sp. (holotype, MACN-N 03), articulated to the three last thoracic vertebrae, in ventral (**A**), dorsal (**B**), and lateral (**C**) views. **D.** Sequence of thoracic vertebrae (2nd–8th) in lateral (right) view. Scale bar = 2 cm.

Among Cenozoic and Recent birds, the following share similarities to *Patagopteryx*.

Tinamiformes: The main similarities noted are the morphology of the cervical vertebrae, the open ilio-ischiatic fenestrae, the large and horizontal postacetabular portion of the ilium, the appearance of the trochanteric crest of the femur, the medial position of the tendinal groove of the tibiotarsus, and a reduced hypotarsus.

Lithornithiformes Houde 1988: This order of birds is, as we see it, very similar to the Tinamiformes and shows the same similarities with *Patagopteryx* as the tinamous, in addition to having a wide planar surface of the lateral portion of the femoral trochanter and lacking a supratendinal bridge of the tibiotarsus. Also, the ilio-ischiatic and ischio-pubic fenestrae may be open in the Lithornithiformes. The elongated acromial process of the scapula may be a feature shared among *Patagopteryx*, Lithornithidae, and *Ambiortus* (Kurochkin, 1985).

Rheiformes: In comparison with *Diogenornis* Alvarenga 1983 from the Paleocene of Brazil, the earliest unquestionable ratite bird, *Patagopteryx* shares the following characteristics: last tho-

Figure 8. Pectoral girdle elements of *Patagopteryx deferrariisi* n. gen., n. sp (holotype, MACN-N 03). **A.** Right scapula. **B.** Left scapula. **C.** Extremitas externalis of the right coracoid in internal view. **D, E.** Fragments identified as the cranial end of clavicles. Scale bar = 2 cm.

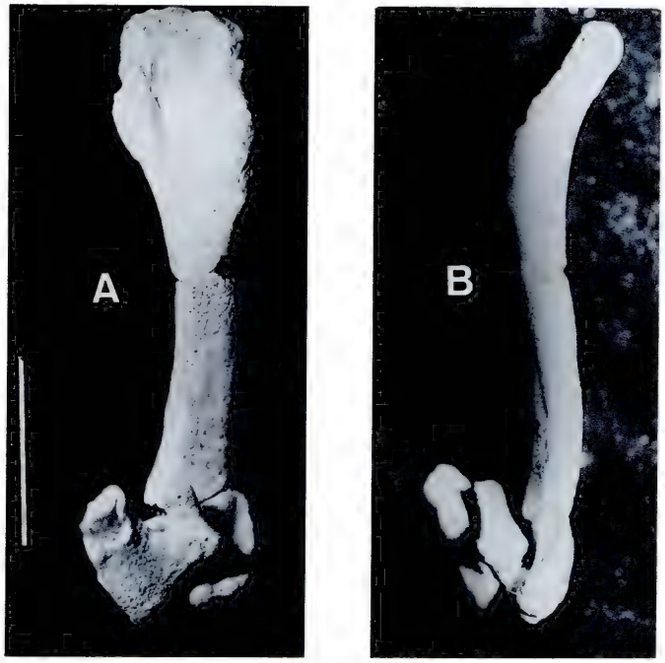

Figure 9. Left humerus of *Patagopteryx deferrariisi* n. gen., n. sp. (holotype, MACN-N 03), with the proximal end of ulna and radius articulated (original position): palmar (**A**) and lateral (**B**) views. Scale bar = 2 cm.

racic vertebrae ventrally flattened; no pneumatic foramen in the humerus; trochanteric crest of the femur expanded anteriorly; large planar surface on the lateral side of femoral trochanter; deep and triangular fossa poplitea; on the tibiotarsus, a robust and anteriorly developed outer cnemial crest, no supratendinal bridge, a rounded external condyle; and a shallow and wide incisura intercondylaris. In comparison with *Rhea*, the similarities noted are nearly the same as those between *Patagopteryx* and *Diogenornis*, but we can also see a similar morphology of the vertebral bodies and the tendency of the *Patagopteryx* ischia to become horizontal and to approach each other medially. The proximal end of the ulna is also very compressed laterally in both rheas and *Patagopteryx*.

Other ratites: The Casuariiformes and Apterygiformes have similarities with *Patagopteryx*, including the distal separation of the ilium, ischium, and pubis; absence of (or vestigial) pneumatic foramen in the humerus; femur with wide planar surface in the lateral region of the trochanter, a trochanteric crest anteriorly developed, and a deep and triangular fossa poplitea; and tibiotarsus with a rounded external condyle, a medially placed tendinal groove, and a wide and narrow incisura intercondylaris. A rather remarkable feature of *Patagopteryx* is that the outer cnemial crest is anteriorly developed (the inner is formed over the outer), a character shared only with ostriches and rheas among all birds.

Naturally, it is important to remember that *Patagopteryx* was

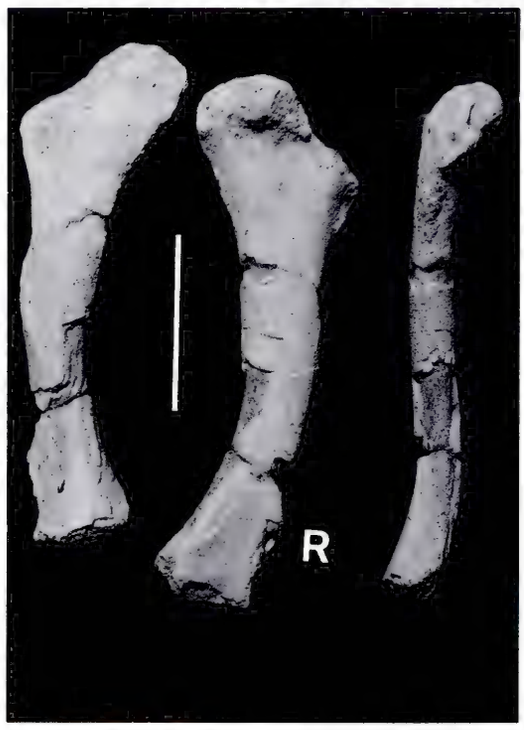

Figure 10. Palmar, anconal, and medial views of the left (**L**) and right (**R**) humeri of *Patagopteryx deferrariisi* n. gen., n. sp. (holotype, MACN-N 03). Scale bar = 2 cm.

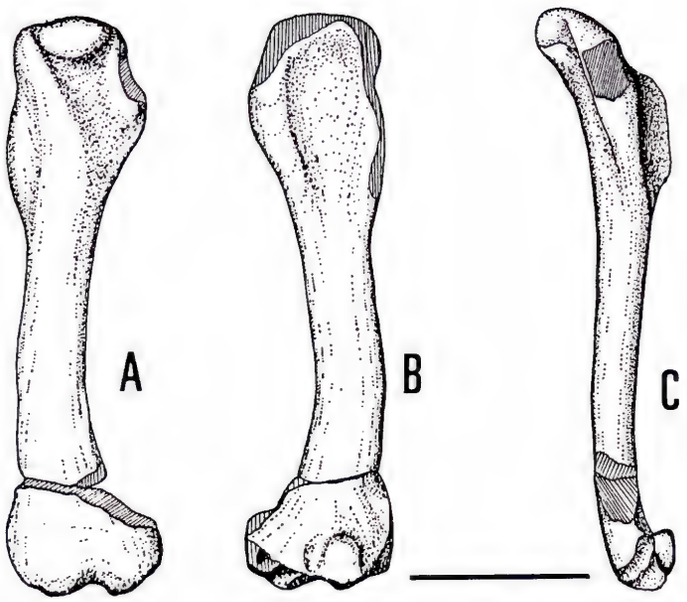

Figure 11. Anconal (**A**), palmar (**B**), and medial (**C**) views of the left humerus of *Patagopteryx deferrariisi* n. gen., n. sp. (holotype, MACN-N 03). Scale bar = 2 cm.

a terrestrial bird, and like all the taxa mentioned here its hindlimbs were much more developed than the wings. Thus, several of the characters mentioned may be attributed to convergence toward the ratites. Nonetheless, two things must be kept in mind. First, none of the other groups of terrestrial birds examined, e.g., several phorusracids, *Cariama* Brisson 1760, *Diatryma* Cope 1876, and species of the Galliformes, share the same similarities as do the ratites and *Patagopteryx*. Second, the foot of *Patagopteryx*, with its long toes and short, flat tarsometatarsus, which may not have been appropriate for running, does not support the idea that the similarities of the tibiotarsus, femur, and pelvis are only convergent with those of ratites.

CONCLUSIONS

The preceding comparison suggests that *Patagopteryx* is an adaptive type close to the Rheiformes and, to a lesser degree, to other ratites and the Tinamiformes. However, there are significant osteological differences, such as the procoelous thoracic vertebrae, the morphology of the ilium, the presence of a hallux, and other features, which lead us to propose the recognition of a new order of birds, the Patagopterygiformes, of uncertain relationships with the ratites.

The presence of *Patagopteryx* in the Coniacian of Patagonia, as a possible primitive new order of cursorial birds, does not nullify the hypothesis of Cracraft (1974) that the ratites differentiated in Gondwana. The biogeographical break between Laurasia and Gondwana that existed during most of the Cretaceous (Lillegraven et al., 1979) was responsible for several endemisms among terrestrial vertebrates of Gondwana (Bonaparte, 1986) and could be responsible for the origin and differentiation of ratite-like birds in South America.

We interpret the presence of paleognathous birds in the lower Tertiary of North America and Europe (Houde and Olson, 1981; Houde, 1986, 1988) as the result of a faunal interchange at the end of the Cretaceous from a South American tinamou-like stock.

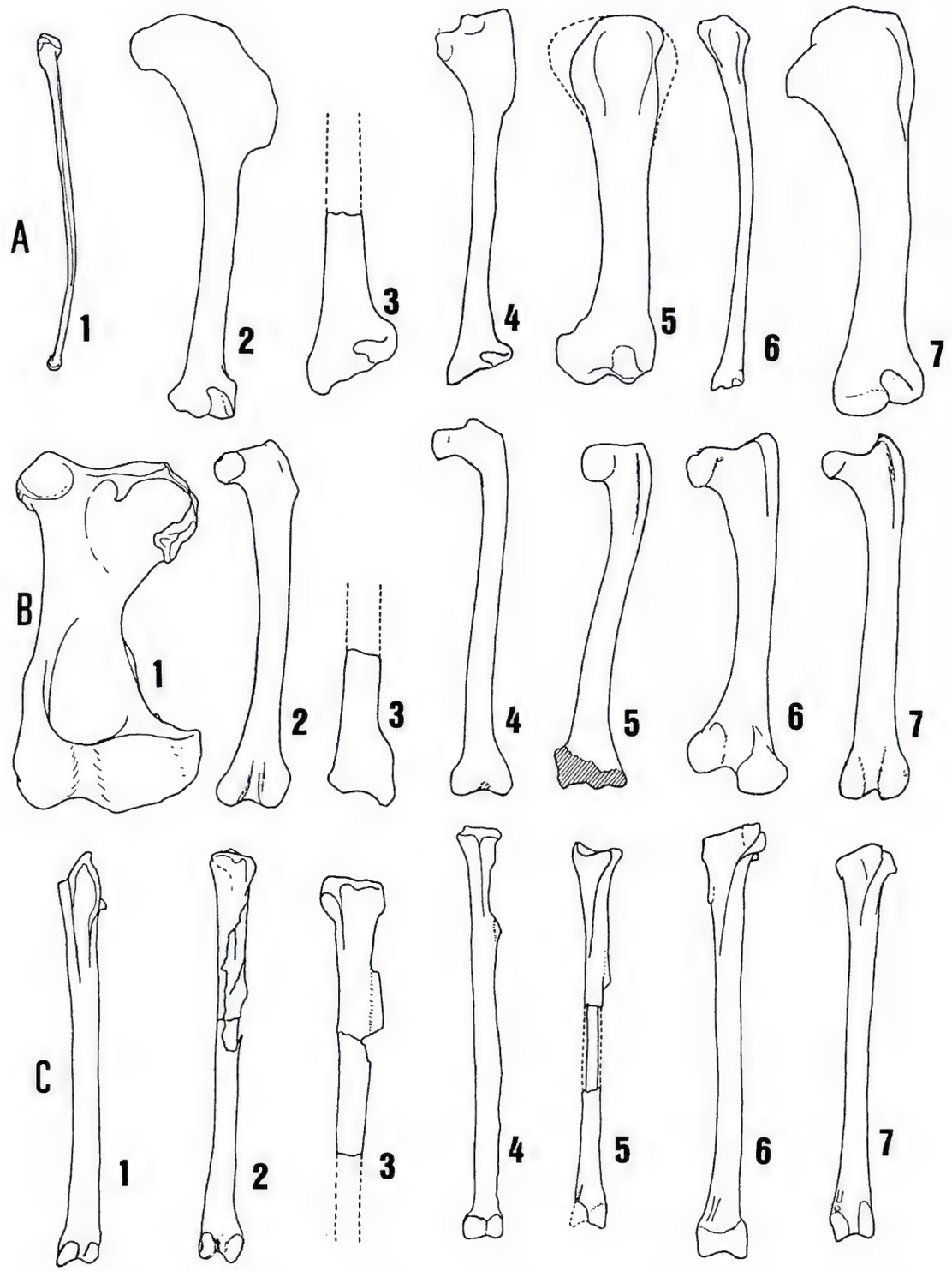

Figure 12. Left humerus (**A**), femur (**B**), and tibiotarsus (**C**). Comparison in anterior view of: **1,** *Hesperornis;* **2,** *Ichthyornis;* **3,** *Alexornis;* **4,** *Enantiornithes;* **5,** *Patagopteryx;* **6,** *Rhea;* **7,** *Tinamus.* Not to scale.

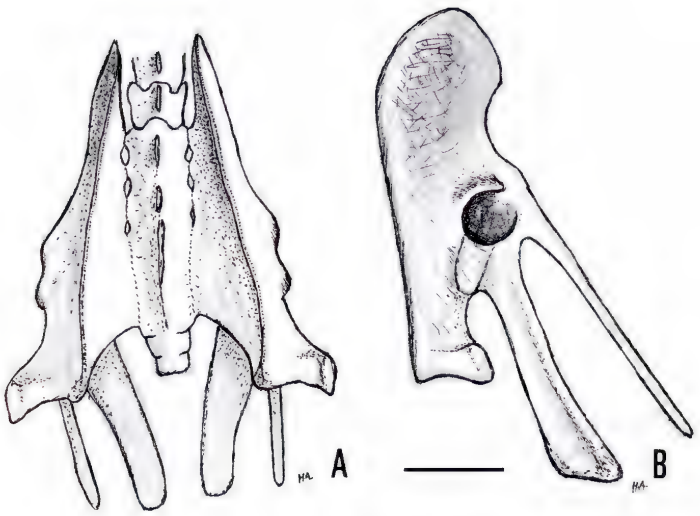

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Figure 13. Restoration of the pelvis of *Patagopteryx*, based on holotype and the unprepared specimen MACN-N 11, in dorsal (**A**) and lateral (**B**) views. Scale bar = 2 cm.

Figure 14. Anterior, posterior, medial, and lateral views of the left (**L**) and right (**R**) femora of *Patagopteryx deferrariisi* n. gen., n. sp. (holotype, MACN-N 03). Scale bar = 2 cm.

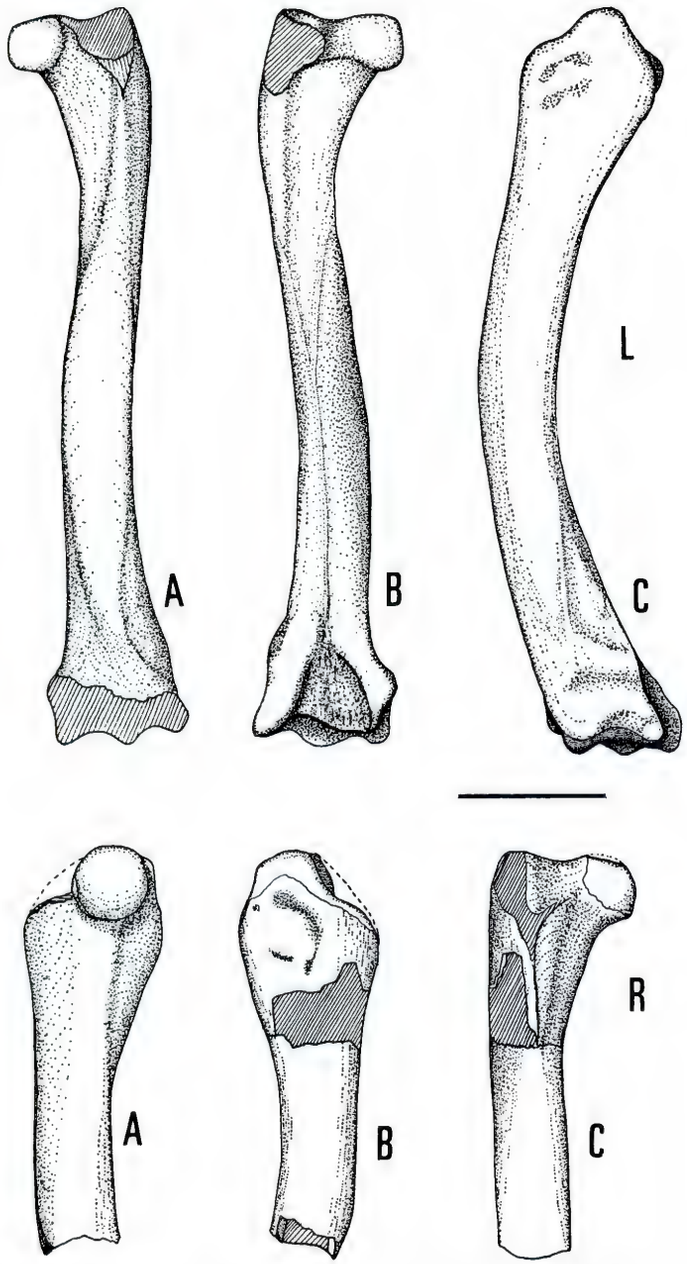

Figure 15. *Patagopteryx deferrariisi* n. gen., n. sp. (holotype, MACN-N 03). Left femur (**L**) in anterior (**A**), posterior (**B**), and lateral (**C**) views; right femur (**R**) in medial (**D**), lateral (**E**), and anterior (**F**) views. Scale bar = 2 cm.

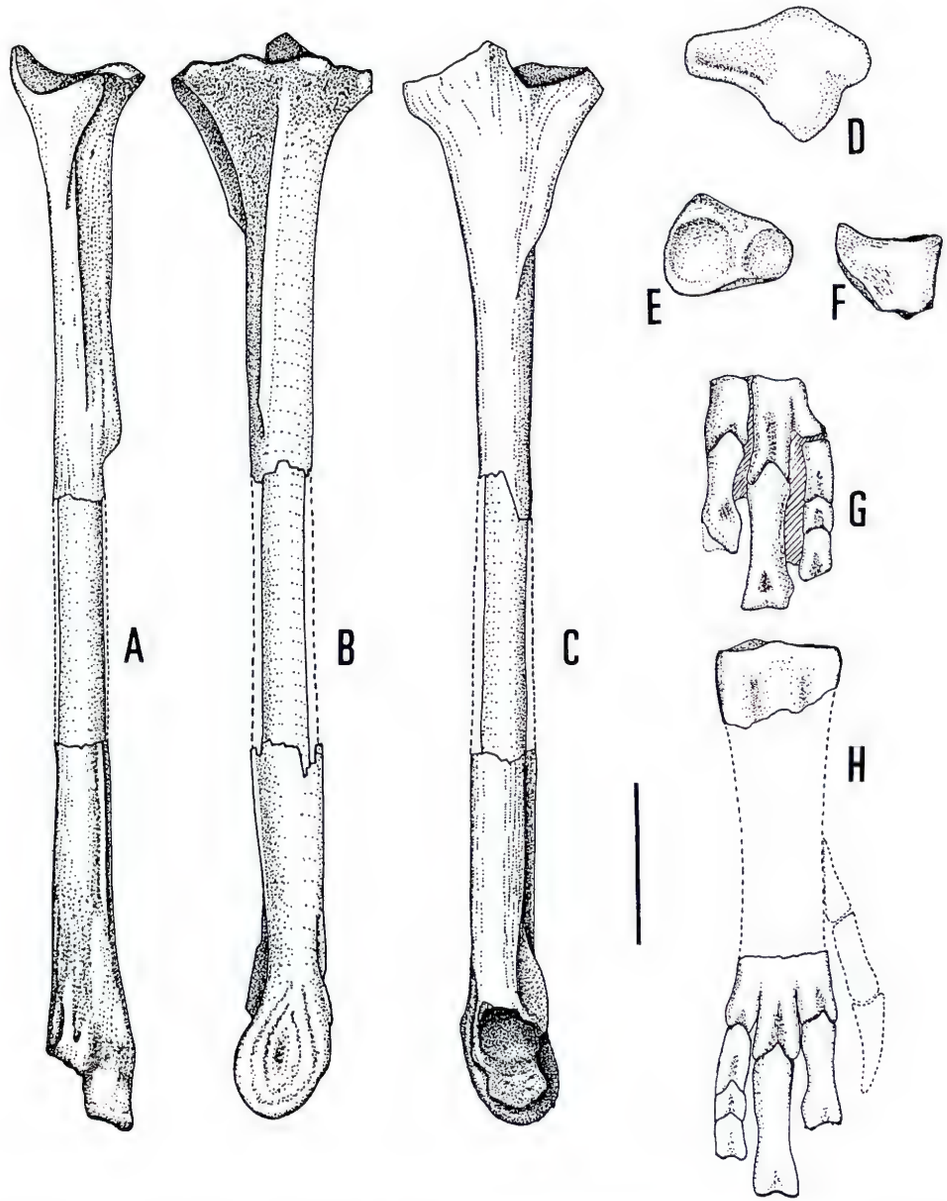

Figure 16. *Patagopteryx deferrariisi* n. gen., n. sp. (holotype, MACN-N 03). Left tibiotarsus in anterior (**A**), lateral (**B**), medial (**C**), and proximal (**D**) views; proximal end of the right tarsometatarsus in proximal (**E**) and lateral (**F**) views; distal end of the left tarsometatarsus (**G**). Reconstruction of the right tarsometarsus (**H**), based on holotype and specimen MACN-N 11. Scale bar = 2 cm.

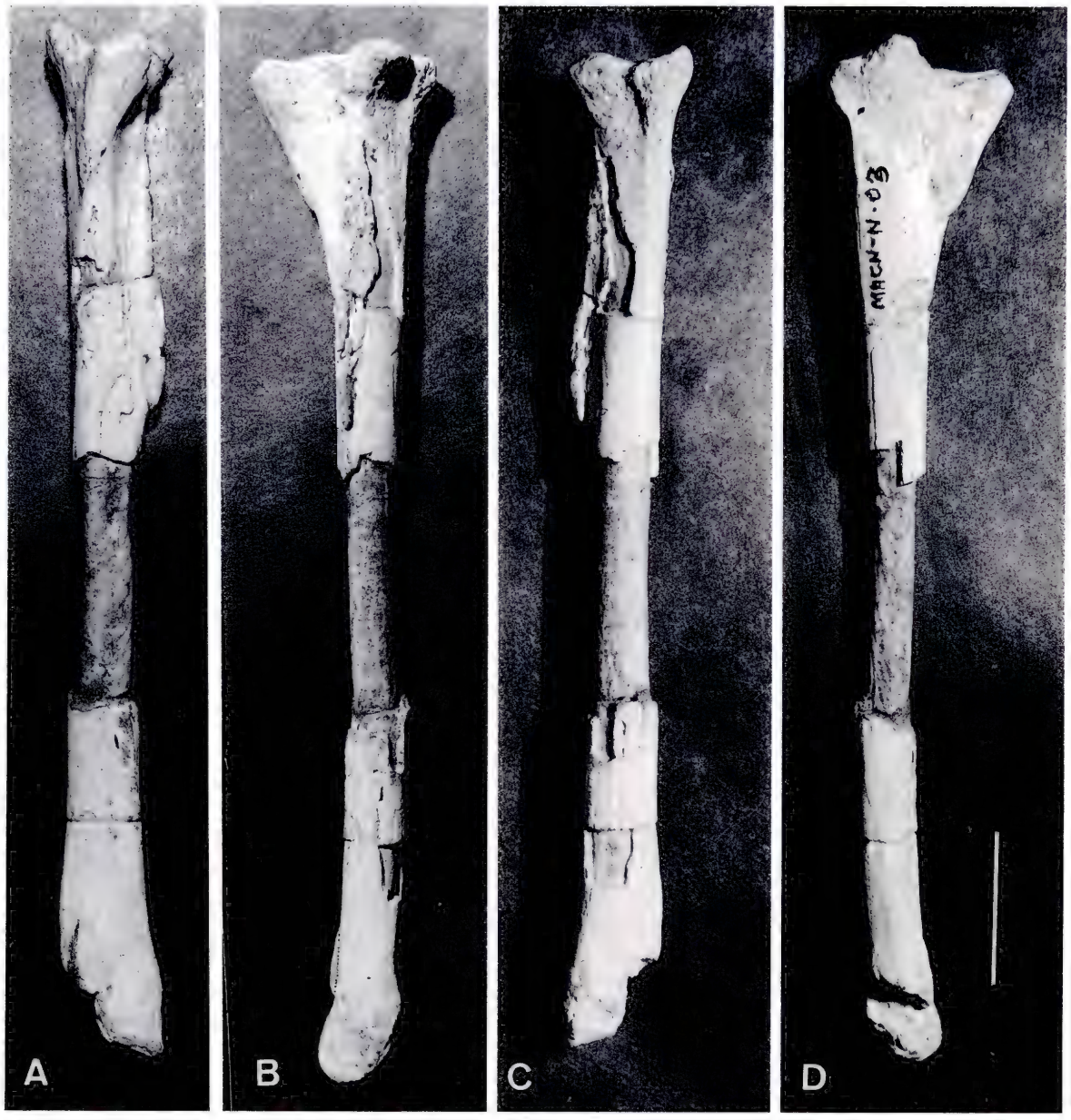

Figure 17. *Patagopteryx deferrariisi* n. gen., n. sp. (holotype, MACN-N 03). Left tibiotarsus in anterior (**A**), lateral (**B**), posterior (**C**), and medial (**D**) views. Scale bar = 2 cm.

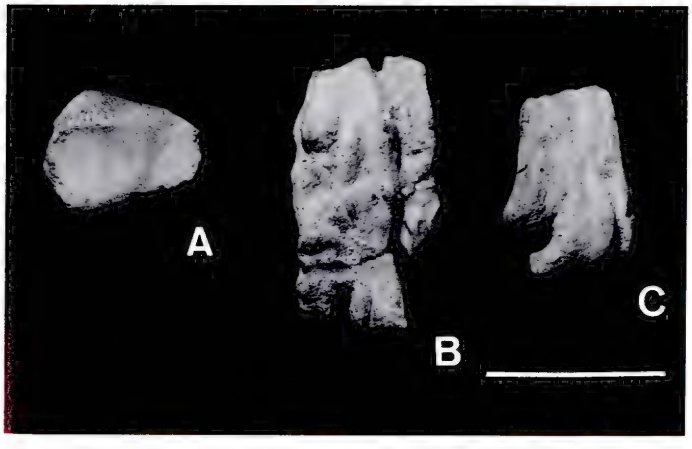

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Figure 18. *Patagopteryx deferrariisi* n. gen., n. sp. **A.** Proximal end of right tarsometatarsus in proximal view (holotype, MACN-N 03). **B.** Distal end of tarsometarsus (holotype, MACN-N 03). **C.** Distal end of tarsometatarsus (referred material, MACN-N 10). Scale bar = 2 cm.

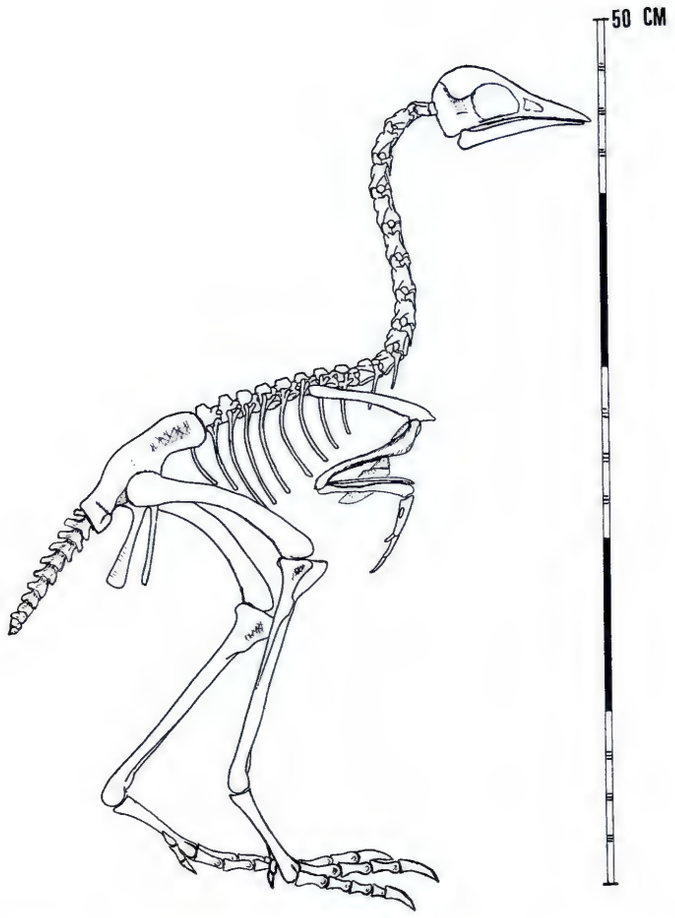

Figure 19. Restoration of skeleton of *Patagopteryx deferrariisi* n. gen., n. sp. Based on holotype and specimen MACN-N 11.

the laboratory of paleontology of the Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina.

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PALEOGENE

BIRDS

THE GALLIFORMES (AVES) FROM THE PHOSPHORITES DU QUERCY (FRANCE): SYSTEMATICS AND BIOSTRATIGRAPHY

Cécile Mourer-Chauviré

ABSTRACT. Several extinct genera of the order Galliformes have been described from the Paleogene "Phosphorites du Quercy" (*Paraortyx, Palaeocryptonyx, Pirortyx,* and *Palaeortyx*), mainly based on fossil humeri. New excavations have produced additional skeletal elements that can be associated with these humeri.

Humeri of the genus *Paraortyx* are associated with coracoids and carpometacarpi with a combination of primitive and derived features. This information suggests that the genus represents a new family, Paraortygidae, which also includes the genus *Pirortyx*.

The species *Palaeocryptonyx depereti* Gaillard, or *Pirortyx depereti* (Gaillard), is transferred to the new genus *Quercymegapodius* and referred to a new family, the Quercymegapodiidae. Another species of the genus, *Quercymegapodius brodkorbi* new species, is described.

True phasianids, placed in the genus *Palaeortyx*, appear only at the end of the Early Oligocene, coinciding with the occurrence of another phasianid, *Schaubortyx*, from Armissan. *Palaeortyx* is represented in the Quercy by three species, all of which persisted into the Early Miocene: *P. brevipes* (=*P. ocyptera*), *P. gallica*, and *P. intermedia*.

RÉSUMÉ. Plusieurs genres de Galliformes avaient été décrits dans le Quercy, *Paraortyx, Palaeocryptonyx, Pirortyx,* et *Palaeortyx,* principalement d'après des humérus. Les nouvelles fouilles dans les Phosphorites du Quercy ont permis de trouver d'autres éléments du squelette qui peuvent être associés à ces humérus.

Dans le genre *Paraortyx* les humérus sont associés à des coracoïdes et à des carpométacarpes de forme primitive et qui permettent de montrer que ce genre représente une nouvelle famille, les Paraortygidae, à laquelle appartient aussi le genre *Pirortyx*.

L'espèce *Palaeocryptonyx depereti* Gaillard, ou *Pirortyx depereti* (Gaillard), est transférée dans le nouveau genre *Quercymegapodius* et classée dans la nouvelle famille des Quercymegapodiidae. Une autre espèce de ce genre, *Q. brodkorbi*, est également décrite.

Les vrais Phasianidae, avec le genre *Palaeortyx*, n'apparaissent qu'à la fin de l'Oligocène inférieur, ce qui coincide avec la présence d'un autre Phasianidae, *Schaubortyx*, dans le gisement d'Armissan, daté exactement du même âge. *Palaeortyx* est représentée dans le Quercy par trois espèces qui se poursuivent toutes les trois dans le Miocène inférieur, *P. brevipes* (=*P. ocyptera*), *P. gallica*, et *P. intermedia*.

Key words: Galliformes, Phosphorites du Quercy, France, Eocene, Oligocene, systematics, biostratigraphy.

INTRODUCTION

The deposits of "Phosphorites du Quercy" are fillings of small karstic networks situated in marine Liassic and Jurassic limestones in the departments of Tarn, Tarn-et-Garonne, Lot, and Aveyron of southwestern France. These limestones emerged and were folded at the end of the Jurassic. The karstic phenomena began during the Late Eocene and, as soon as the sinkholes formed, they filled with clayish deposits, rich in calcium phosphate and incorporating numerous vertebrate remains (Gèze, 1938, 1939, 1949). The calcium phosphate was mined for use as fertilizer from 1865 to about 1900. During the course of this mining, fossil vertebrates were gathered, but precise data as to which sinkhole they were collected from were not kept. Fossil birds found during these early excavations were described by Lydekker (1891), Milne-Edwards (1892), and Gaillard (1908, 1939). Recent excavations undertaken by research workers of the Montpellier and Paris VI Universities produced fossil birds associated with micromammals, and their age is therefore accurately known. These associated mammalian faunas indicate an age ranging from Late Eocene to Late Oligocene. The purpose of the present study is to revise the systematics of the previously described galliforms from Quercy and to describe several new taxa.

GENERAL SUMMARY OF THE FOSSIL HISTORY OF GALLIFORMES

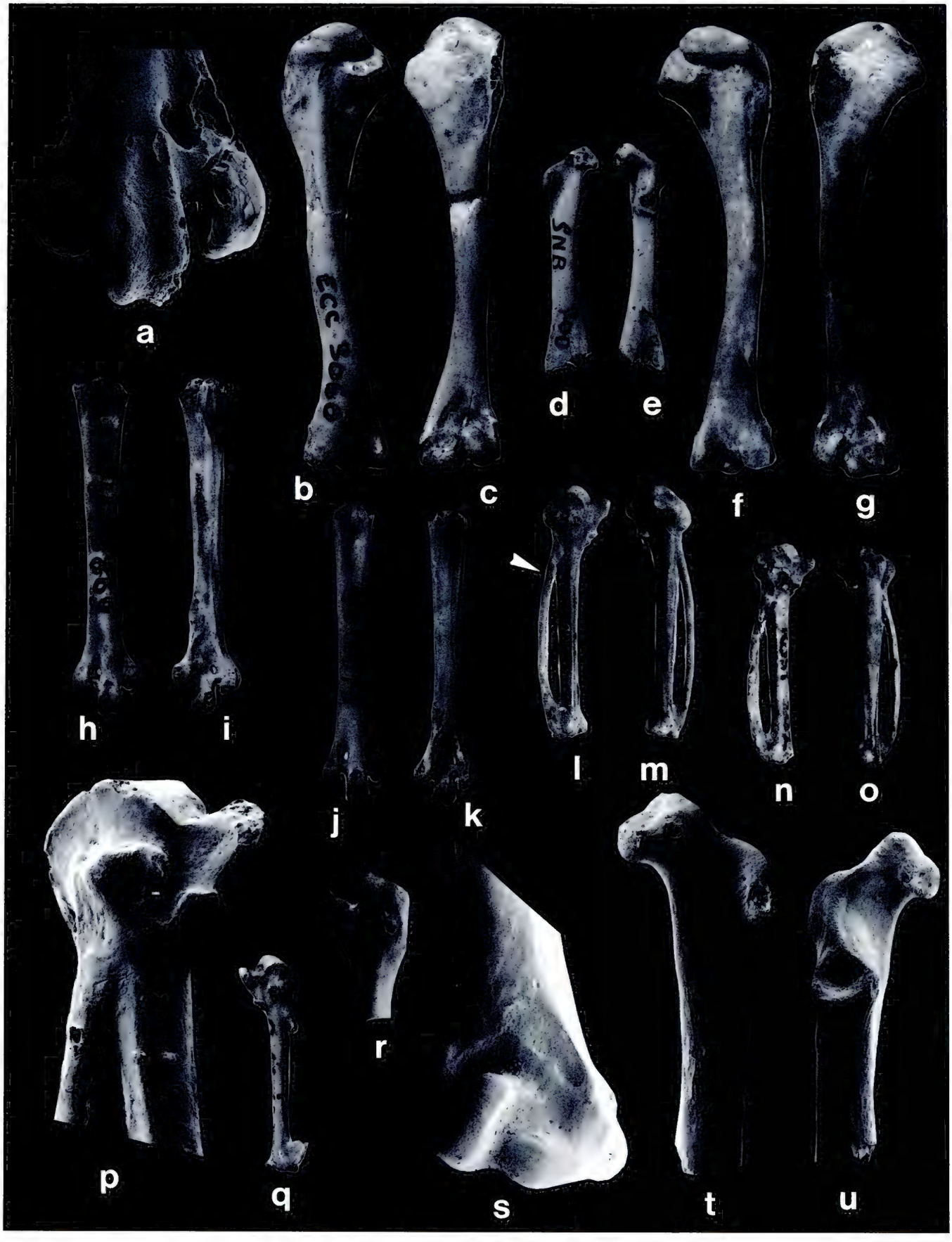
A detailed account of the fossil record of Galliformes is to be found in Olson (1985). Until now, the Galliformes were known as fossils by one extinct and three Recent families.

The extinct family Gallinuloididae includes the earliest known galliform, *Gallinuloides wyomingensis* Eastman 1900, from the Lower Eocene of Wyoming. Two other extinct genera have been placed in this family, *Procrax* Tordoff and Macdonald 1957, from the Lower Oligocene of South Dakota, and *Taoperdix* Milne-Edwards 1869, from the Oligocene of France and Miocene of Germany.

The Recent family Cracidae is known from the Upper Oligocene (Brodkorb, 1964) or the Lower Miocene (Olson, 1985) of North America.

The Recent family Megapodiidae is as yet unknown from the Tertiary. I had earlier indicated the occurrence of Megapodiidae in the Quercy deposits (Mourer-Chauviré, 1982), but now I think that the Quercy forms are more primitive than the Recent megapodes and, in this present work, I put them in a new, extinct family, the Quercymegapodiidae.

The Recent family Phasianidae includes five subfamilies.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1. The Numidinae have been known since the Late Eocene, being first recorded in Mongolia with the species *Telecrex grangeri* Wetmore 1934, which was based on an incomplete femur corresponding to "one of the more advanced Galliformes" (Olson, 1985:117). However, the forms from the Eocene of Quercy, for example, may have advanced features associated with primitive features, and the femur is not a very diagnostic element. The assignment of *Telecrex* to Numidinae should therefore be considered with caution.

2. The Meleagridinae have been known since the Early Miocene, first reported from North America (Steadman, 1980).

3. The Tetraoninae have been known since the Early Miocene, first reported from North America, but Olson (1985) considers that their early assignments should be carefully revised. In Europe, the Tetraoninae have been known only since the Early Pliocene (Janossy, 1976).

4. Two Oligocene forms have been attributed to the Odontophorinae: *Nanortyx inexpectatus* Weigel 1963, from the Lower Oligocene (lowermost Chadronian) of Saskatchewan (which may be referable to the uppermost Upper Eocene), and an Odontophorine from the Middle Oligocene of Colorado (Tordoff, 1951). *Nanortyx* shows some similarities with some of the Quercy forms. Other Odontophorinae are known from the Miocene of North America.

5. The earliest known Phasianinae appear at the end of the Early Oligocene with the genera *Palaeortyx* Milne-Edwards 1869, in the Quercy, and *Schaubortyx* Brodkorb 1964, at Armissan, both in southern France.

Several genera of the Phasianidae have been described by Harrison and Walker (1977, 1979a, 1979b) from the Lower Eocene to the Lower Oligocene of England, but the material does not allow an attribution to a distinct subfamily.

The Quercy material is very important for the knowledge of the early history of Galliformes. There are abundant three-dimensional bones, most of which have been found in the same sites and can be associated with each other, and the sites are accurately situated on the chronological scale. The occurrence of bones with advanced features associated with other skeletal elements with primitive features makes it possible to describe two new, extinct families. The evolutionary implications of this fossil material are discussed at the end of this paper.

MATERIAL AND METHODS

The fossil material studied in the present work is conserved in the following museums: Muséum national d'Histoire naturelle (MNHN), Paris; Musée Guimet d'Histoire naturelle (MGHN), Lyon; Laboratoire de Paléontologie de l'Université des Sciences et Techniques du Languedoc (USTL), Montpellier; University of Marseille; Muséum d'Histoire naturelle (MHN), Montauban, in France; and Museum of Natural History (MNH), Basel, in Switzerland.

The comparative material used comes from the collections of the Laboratoire d'Anatomie comparée (MNHN Paris); the Département des Sciences de la Terre de l'Université Claude Bernard, Lyon 1; the Musée Guimet d'Histoire naturelle de Lyon; the Pierce Brodkorb Collection at the University of Florida, Gainesville; the National Museum of Natural History, Washington, D.C.; the American Museum of Natural History, New York; the Museum of Zoology of the University of Michigan; and the Peabody Museum of Natural History, Yale University.

The anatomical terminology generally follows Howard (1929) but also Ashley (1941), Ballmann (1969b), and Baumel (1979).

The measurements are given in millimeters. When the bone is incompletely preserved, the measurement is an estimation, indicated by the abbreviation c. (*circa*). The various measurements are explained in Mourer-Chauviré (1975).

SYSTEMATICS

Order Galliformes Temminck 1820

Family Gallinuloididae Lucas 1900

Genus *Taoperdix* Milne-Edwards 1869

Taoperdix sp.

Figure 1a

MATERIAL. New excavations: USTL Montpellier: Le Bretou, Upper Eocene, left tarsometatarsus, distal end, BRT 1034.

DESCRIPTION AND COMPARISONS. A very small galliform is present in the deposits of Le Bretou. This form is represented by a single distal end of tarsometatarsus, which has been described in detail in a monograph devoted to the locality of Le Bretou (Mourer-Chauviré, 1988). On this tarsometatarsus, the trochleae are situated along a rather curved line; the internal trochlea is slightly shorter than the external trochlea, and it does not protrude posteriad to any great extent; the distal foramen is widely open; and on the posterior face a large depression occupies virtually the entire width of the bone and extends distad to the level of the distal foramen.

This tarsometatarsus differs from that of all other galliforms by two features: The length of the internal trochlea is almost the same as the length of the external trochlea, and the presence of a large depression on the posterior face. With regard to the first feature, it resembles the genera *Gallinuloides* Eastman 1900 and *Taoperdix* Milne-Edwards, which have been put in the family Gallinuloididae (Lucas, 1900; Tordoff and Macdonald, 1957; Ballmann, 1969b). I provisionally refer this specimen to

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Figure 1. Cf. *Taoperdix* sp.: **a**, left tarsometatarsus, USTL, BRT 1034, anterior view, ×11. *Quercymegapodius depereti:* left humerus, USTL, ECC 3060, in anconal (**b**) and palmar (**c**) views, ×2; right coracoid, cranial end, USTL, SNB 700, in ventral (**d**) and dorsal (**e**) views, ×2; right humerus, MHN Montauban, MA 5, in anconal (**f**) and palmar (**g**) views, ×2; almost complete right tarsometatarsus, MNHN Paris, QU 15869, in anterior (**h**) and posterior (**i**) views, ×2; incomplete right tarsometatarsus, MNHN Paris, QU 16973, in anterior (**j**) and posterior (**k**) views, ×2; left carpometacarpus, MNHN Paris, QU 15673, in internal (**l**; the arrow indicates the position of a small hook-like tubercle on the os metacarpale minus) and external (**m**) views, ×2. *Quercymegapodius brodkorbi* n. sp.: holotype left carpometacarpus, almost complete, USTL, ROS 1, 202, in internal (**n**) and external (**o**) views, ×2, and detail of the proximal part (**p**), ×7; almost complete right carpometacarpus, MNH Basel, Q.W. 1574, in internal (**q**) view, ×2; right humerus, proximal end, MNHN Paris, QU 17030, in anconal (**r**) view, ×2; detail of the right humerus, distal end, USTL, BFI 1850, in palmar (**s**) view, ×7; left coracoid, cranial end, USTL, BFI 1849, in ventral (**t**) and dorsal (**u**) views, ×6.

cf. *Taoperdix* sp. Measurements (mm) are as follows: distal width, 3.8; distal depth, 2.5 (Mourer-Chauviré, 1988).

Paraortygidae new family

TYPE GENUS. *Paraortyx* Gaillard 1908.

DIAGNOSIS. Galliform, with coracoid with hollow, cup-like scapular facet, with an oval outline; humerus with two fossae, the tricipital fossa and the pneumatic fossa, with the former wide and deep in *Paraortyx*, wide and shallow in *Pirortyx;* humeral head not connected by ridge to internal tuberosity; relatively short carpometacarpus with a robust metacarpale majus; proximal part of carpometacarpus strongly developed, with a rounded carpal trochlea; tarsometatarsus with a hypotarsus not very different from that of Recent phasianids, with two main ridges, internal and external, and a second external ridge that is less developed and shorter.

INCLUDED GENERA. Type genus; *Pirortyx* Brodkorb 1964.

TEMPORAL AND GEOGRAPHIC DISTRIBUTION. Upper Eocene to Upper Oligocene of Phosphorites du Quercy, France.

BACKGROUND. In 1891, Milne-Edwards presented a paper on the birds of the Phosphorites du Quercy at the 2nd International Ornithological Congress in Budapest. In this paper, he described two species of the genus *Palaeortyx, P. ocyptera* and *P. cayluxensis*. The type species of this genus is *P. gallica* Milne-Edwards 1869, from the Miocene of Saint-Gérand-le-Puy. The same year, Lydekker (1891) described a species of *Palaeortyx, P. cayluxensis* from the Phosphorites before Milne-Edwards' study appeared (issued in 1892), so the name *P. cayluxensis* Lydekker 1891 has priority over *P. cayluxensis* Milne-Edwards 1892.

Because it was generally recognized that *Palaeortyx cayluxensis* Lydekker was synonymous with *P. ocyptera* Milne-Edwards 1892, the species name *P. cayluxensis* Milne-Edwards was replaced by *P. gaillardi* Lambrecht 1933. Two species of *Paleortyx* were then considered as present in the Quercy deposits, *P. cayluxensis* Lydekker and *P. gaillardi* Lambrecht, with the genus *Palaeortyx* being placed in the family Phasianidae (Brodkorb, 1967).

I have examined the holotype of the species *Palaeortyx cayluxensis* described by Milne-Edwards (=*P. gaillardi* Lambrecht), and I believe that it is referable to *Paraortyx lorteti* Gaillard 1908.

On the other hand, during the new excavations at Quercy, numerous galliform remains from a single species were found in the locality of Itardies. Humeri of this form appear to have some derived characters, i.e., a deeply excavated tricipital fossa, but the associated coracoids and carpometacarpi appear to have some primitive features. The coracoid has a hollow, oval, cup-like scapular facet that is not found in any Recent galliforms (including the families considered as primitive within this group, such as the Megapodiidae and the Cracidae). This unusual type of coracoid is to be found in all Upper Eocene and Lower Oligocene Quercy deposits, whereas the typical coracoid of modern galliforms is found only in Upper Oligocene sites. The carpometacarpus shows a weakly developed intermetacarpal apophysis, as in all megapodes and cracids and some phasianids. I consider this to be a primitive character.

The humerus of the Itardies galliform corresponds to the type humerus of the species *Palaeortyx cayluxensis* Milne-Edwards, which became *P. gaillardi* Lambrecht, and also to the type humerus of the species *Paraortyx lorteti* Gaillard. Because this humerus with derived characters is associated with coracoids and carpometacarpi with primitive characters, it is not possible to maintain this form in either the family Phasianidae, where the genus *Palaeortyx* belongs, or in the family Cracidae, where Brodkorb (1964) placed the genus *Paraortyx*. It is therefore necessary to create a new family for this genus: the Paraortygidae.

Paraortyx Gaillard 1908

1892	pars	*Palaeortyx* Milne-Edwards, p. 72.
1908	pars	*Palaeortyx* Milne-Edwards: Gaillard, p. 100.
1908		*Paraortyx* Gaillard, p. 104.
1933	pars	*Palaeortyx* Milne-Edwards: Lambrecht, p. 456.
1933		*Paraortyx* Gaillard: Lambrecht, p. 456.
1939	non	*Paraortyx* Gaillard: Gaillard, p. 24 (see Remarks about *Paraortyx brancoi*).
1964	pars	*Ludiortyx* Brodkorb, p. 298.
1964		*Paraortyx* Gaillard: Brodkorb, p. 299.

TYPE SPECIES. *Paraortyx lorteti* Gaillard 1908.

DIAGNOSIS. By Milne-Edwards (1892:72) for the species *Palaeortyx cayluxensis:* "Une seconde espèce de *Palaeotyx* [*sic*] est indiquée par un humérus semblable par ses caractères essentiels à celui que je viens de décrire (*P. ocyptera*), mais différent par ses dimensions et par plusieurs particularités anatomiques. Cet os est notablement plus fort et plus élargi dans sa partie supérieure. La tête articulaire est plus renflée surtout en dehors, la surface bicipitale est plus étendue, la fosse du triceps est très large et ne se continue pas en bas par une dépression triangulaire limitée par des bourrelets saillants; elle se continue au contraire sans ressauts avec le corps de l'os. Je ne puis parler du caractère de l'extrémité inférieure car cette partie est brisée sur l'exemplaire unique que j'ai entre les mains . . ."

DIAGNOSIS. By Gaillard (1908:104) for the genus *Paraortyx:* "L'humérus des *Paraortyx* n'a pas de foramen pneumatique. Néanmoins l'extrémité supérieure est entièrement excavée par les deux fosses sous-trochantérienne et tricipitale qui se prolongent jusqu'à la paroi de la surface articulaire, et ne sont séparées l'une de l'autre que par une mince cloison osseuse. La crête pectorale est, en outre, beaucoup moins recourbée en dedans que chez les *Palaeortyx, Ortyx* et *Perdix* et l'extrémité inférieure de l'humérus est plus dilatée transversalement."

INCLUDED SPECIES. Type species; *Paraortyx brancoi* Gaillard 1908.

DISTRIBUTION. Upper Eocene and Lower Oligocene of the Phosphorites du Quercy, France.

DESCRIPTION AND COMPARISONS. Coracoid. The coracoid (Figs. 2c, d, 5c) has a hollow scapular facet, having the form of an elliptical cup with its long axis at a slight angle to the horizontal. The acrocoracoid has the characteristic shape of the acrocoracoid of the galliforms, which cannot be confused with that of any other group of birds. It is not very curved on the internal side, and it does not show pneumatic foramina. The procoracoid projects very slightly. The coracoidal fenestra is absent. The shaft of the bone is flattened and elliptical in cross-section. On the dorsal side, there is a shallow depression above the sternal facet. This facet ends in a sharp point at the internal distal angle. The sternocoracoidal process is well developed on specimen MGB 1547 (Fig. 2c, d), but it is seldom preserved.

On the ventral side, the acrocoracoid forms a small ledge compared to the surface of the shaft.

Extra-group comparisons show that the presence of a deep, cup-like scapular facet is a primitive character in birds. Indeed, this cup-like scapular facet is found in a great number of Recent

birds such as the Sphenisciformes, the Gaviiformes, most of the Ciconiiformes, the Anseriformes, most of the Gruiformes, the Charadriiformes, among the Columbiformes in the Pteroclididae, and the Apodiformes (I did not have the opportunity to check for this character in the Trochilidae).

In the Recent ratites (Struthioniformes, Rheiformes, Casuariiformes, and Apterygiformes), it is not possible to see the shape of the articulation between the scapula and the coracoid because these two bones are fused together in a scapulocoracoid, but the scapular facet is hollow in the Lithornithiformes, paleognathous birds of the Paleocene and Eocene (Houde, 1988). The scapular facet is also deep in Mesozoic birds such as *Ichthyornis* Marsh 1872 and *Hesperornis* Marsh 1872 (Martin, 1987).

It is important to note that the hollow, cup-like scapular facet exists in the Anseriformes, which most recent works on systematics consider as the sister-group of the Galliformes (Sibley et al., 1988).

This deep, concave, scapular articulation has been secondarily lost in a great number of different lineages, which include the Tinamiformes, the Podicipediformes, most members of the Procellariiformes and Pelecaniformes, all Recent species of Galliformes, the Columbidae, the Psittaciformes, most of the Cuculiformes (it is present in Opisthocomidae), the Strigiformes, most of the Caprimulgiformes, the Coliiformes, the Trogoniformes, practically all of the Coraciiformes, the Piciformes, and the Passeriformes.

It is possible to consider the deep, cup-like scapular facet as the primitive condition in birds because, if it was the derived condition, this would imply that it has appeared independently a great number of times in different lineages. It is much easier for a character to be independently lost numerous times than to be acquired independently numerous times. This primitive character, which exists in the oldest galliforms from the Phosphorites du Quercy, also exists in the unique galliform specimen, represented by a postcranial skeleton on a slab, from the Middle Eocene of Messel, in Germany.

The coracoid of *Paraortyx* can be immediately distinguished from that of *Palaeortyx*, which does not have a hollow scapular facet.

Scapula. The scapula (Fig. 2h, i) has a rounded, tubercle-like coracoidal articulation that is very distinct from the glenoid facet and a very sharp acromion.

Humerus. The humerus (Figs. 2a, b, 3, 5a, b, d) of *Paraortyx* has been described by Milne-Edwards (1892) and Gaillard (1908), but it is not very easily distinguished from that of *Palaeortyx*. The main difference is that in *Palaeortyx*, on the anconal surface, the humeral head presents an extension that joins the internal tuberosity. This extension forms a ridge, which is found in all extant galliforms and which closes the capital groove, thus preventing its communication with the tricipital fossa. In *Paraortyx*, there is no ridge between the humeral head and the internal tuberosity; i.e., the capital groove opens into the tricipital fossa. The bottom of the tricipital fossa is lower than the bottom of the tricipital groove, but there is no ridge (Fig. 3).

In *Palaeortyx*, the tricipital fossa is deeper and goes farther inside the humeral head. Also, in this genus the tricipital fossa extends distad obliquely compared to the long axis of the bone, and it is limited on the external side by a well-developed ledge. In *Paraortyx*, the tricipital fossa does not extend distad so obliquely, and it is limited on the external side by a less pronounced ledge (Fig. 3), although there is some individual variation. Some specimens have a tricipital fossa that extends obliquely and has a ledge as pronounced as in *Palaeortyx*.

In *Palaeortyx*, as described by Milne-Edwards (1892:71), the tricipital fossa extends distad: "by a depression with a triangular form, the angle of which is directed downward and where the two sides are marked by projecting rims," whereas on the holotype of *Palaeortyx cayluxensis* (=*Paraortyx lorteti*) Milne-Edwards indicated that the tricipital fossa extends "on the contrary without any rims" toward the shaft of the bone. This feature does indeed exist in the holotype, but it is not present in all specimens of the genus *Paraortyx*.

Specimens of *Paraortyx* also lack a pneumatic foramen in the bottom of the pneumatic fossa.

On the anconal surface, the deltoid crest is not very protrudent and its point is slightly curved on the internal side, whereas in *Palaeortyx* it forms a more developed hook. The bicipital surface and the bicipital furrow are not distinctly separated. The ligamental furrow is short, restricted to the most internal part of the bone, and ends in a deep dimple.

At the distal end, on the palmar face, the impression of m. brachialis anticus is deeply marked and the ectepicondylar prominence is very protrudent. On the anconal face, the entepicondyle is very distinct and projects distad strongly, whereas it does not project so much in *Palaeortyx*.

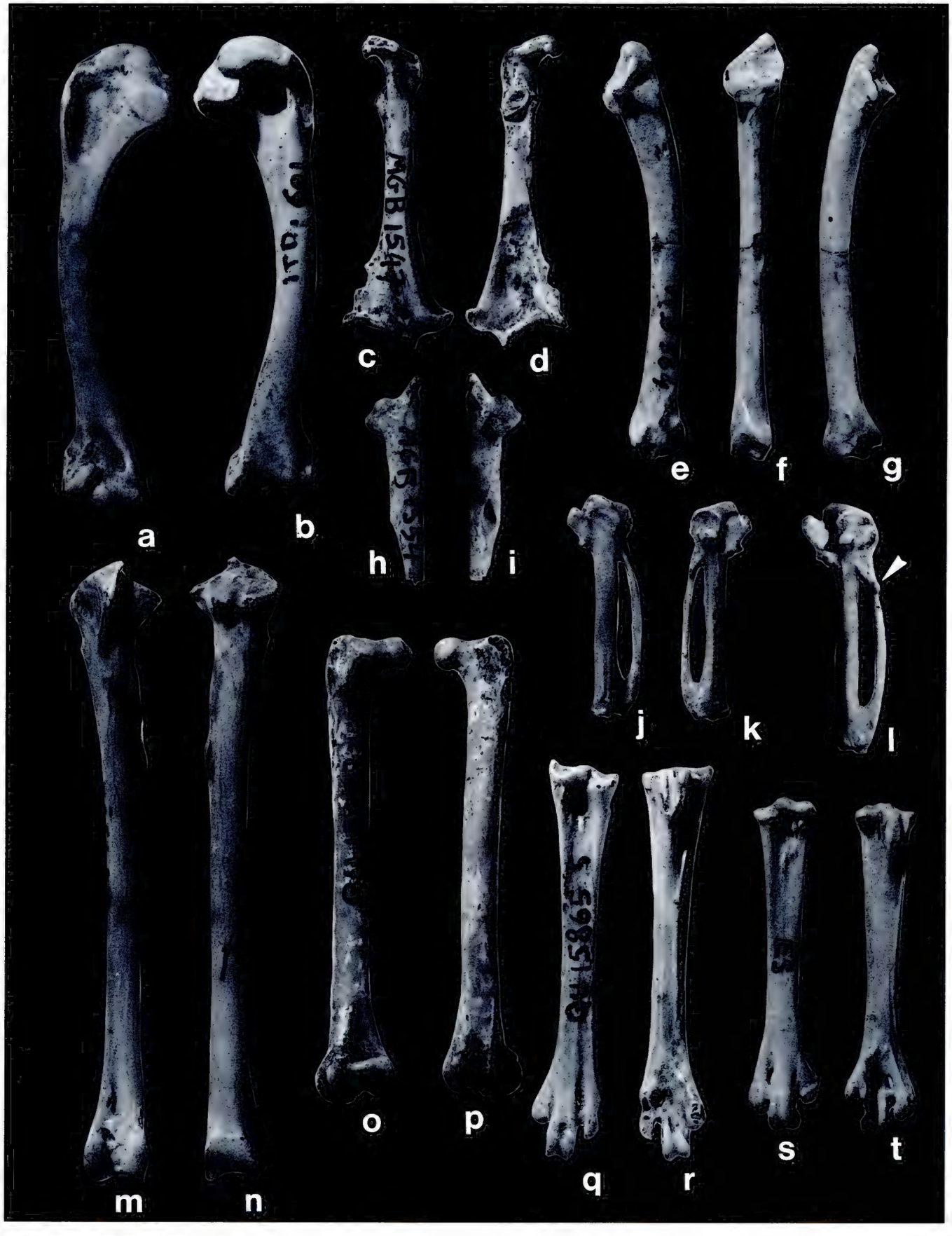
Contrary to the descriptions of Milne-Edwards (1892) and Gaillard (1908), the humerus of *Paraortyx* does not present a proximal and a distal end proportionally wider than in *Palaeortyx*. The ratios (proximal width × 100)/total length and (distal width × 100)/total length are similar in the two genera, as can be seen below:

	(proximal width × 100)/ total length	(distal width × 100)/ total length
Paraortyx lorteti	mean 25.6 (n = 9)	19.7 (n = 9)
Paraortyx brancoi	mean 24.9 (n = 2)	19.0 (n = 2)
Palaeortyx brevipes	mean 24.9 (n = 11)	19.2 (n = 11)
Palaeortyx gallica	mean 26.4 (n = 2)	19.8 (n = 3)
Palaeortyx intermedia	24.0 (n = 1)	19.3 (n = 1)

Extra-group comparisons show that the presence of an extension of the humeral head joining the medial crest of the internal tuberosity (medial bar of Ashley, 1941) and closing the capital groove exists only in Recent galliforms. In Recent tinamiforms, there is not really an extension of the humeral head but, rather, at the same place, there is an attachment for the ligamentum scapulohumerale (Ballmann, 1969b:20, fig. 7, B2) that separates the capital groove from the tricipital fossa. In all other birds, Recent or fossil, the capital groove communicates with the tricipital fossa. The absence of this ridge therefore constitutes the primitive character in birds. The closing of the capital groove and its subsequent separation from the tricipital fossa appears to have been independently acquired, and in a somewhat different way, in the Tinamiformes and in the Galliformes by convergence, perhaps because of the similitude of their way of life.

I think that the absence of this ridge in the Paraortygidae is the primitive condition, rather than a reversal to a primitive condition, because the humeri of *Paraortyx* are associated with a primitive type of coracoid, and if we were to propose a reversal to a primitive condition for the humerus, we would also have to propose a reversal to a primitive condition for the coracoid, and this is not the most parsimonious solution.

Ulna. The ulna (Fig. 2e–g) is short and curves strongly inward, and the shaft is flattened on the internal side as in all the gal-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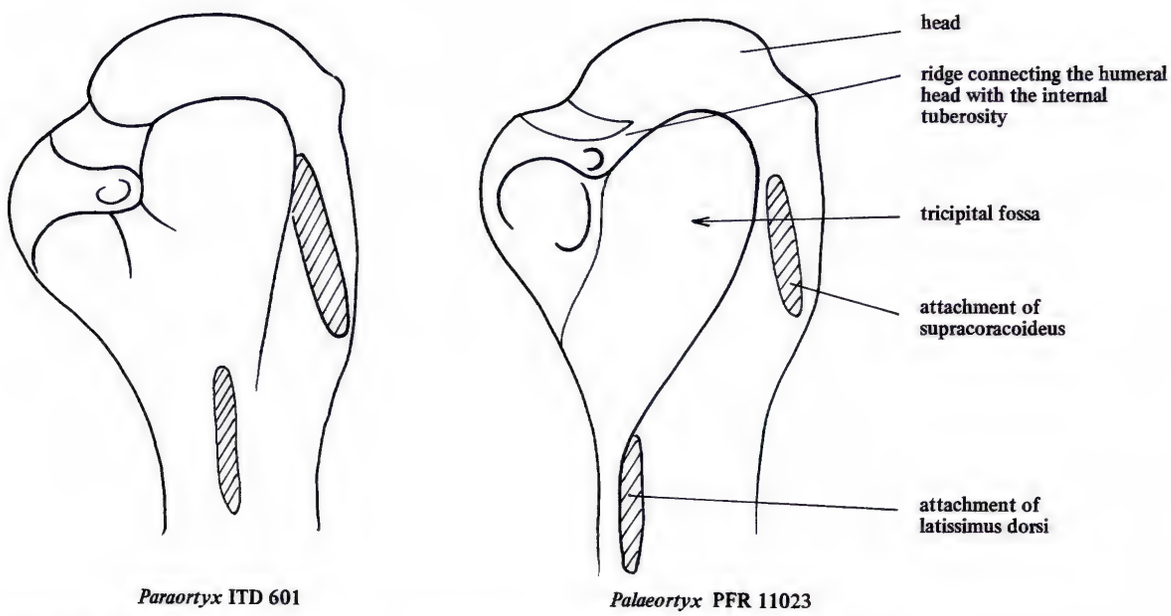


Figure 3. Drawing showing the differences between the humeri of *Paraortyx* and *Palaeortyx*.

liforms. At the proximal end, the internal cotyla is more or less rounded, whereas in *Palaeortyx* it is proximodistally elongated. The external cotyla is also shorter and more protrudent on the external side than in *Palaeortyx*. In *Paraortyx*, the shaft is proportionally more robust than in *Palaeortyx*. In contrast to members of the family Cracidae, the ulnae of *Paraortyx* spp. are shorter than the humeri (Table 1; Fig. 2).

Carpometacarpus. The carpometacarpus (Fig. 2j–l) is relatively short with a robust metacarpale majus. The proximal end is rather well developed, and the carpal trochlea is rounded. The process of the alular metacarpal is not very protrudent. The depressio muscularis interna (Ballmann, 1969b) is generally shallow. The intermetacarpal tuberosity is very rudimentary. There is a small tubercle on the internal side of the metacarpale minus, below the level of fusion with the metacarpale majus, which is well developed in one specimen (Fig. 2l), but it does not present a hook-like, distad-directed shape, as it is found in another genus present in the Quercy. This carpometacarpus is easy to distinguish from that of *Palaeortyx* by the almost complete absence of an intermetacarpal tuberosity and by its much more robust form.

Femur. The femur (Fig. 2o, p) has a characteristic galliform shape, i.e., remarkably elongated and strongly curved with a posteriorly directed concavity. As in the genus *Palaeortyx*, there are no pneumatic foramina distal to the trochanter. Proportionally, the femoral head is slightly smaller in *Paraortyx* than in *Palaeortyx* and less protrudent compared to the proximal articular surface.

Tibiotarsus. There is no complete tibiotarsus from Itardies, but I have attributed to *Paraortyx lorteti* a complete specimen, QU 15684 (Fig. 2m, n), from the Paris MNHN. The main long bones of *Paraortyx lorteti* are similar in size to those of *Palaeortyx gallica*, but this tibiotarsus is proportionally shorter and more robust (Tables 1, 3). The proximal ends of tibiotarsi from Itardies show an external articular surface that is more globular than those of the genus *Palaeortyx*.

Tarsometatarsus. The tarsometatarsus (Fig. 2q–t) is slender. The hypotarsus has three calcaneal ridges: an internal ridge that projects farthest posteriad, an external ridge that is less protrudent, and a smaller, less developed, and shorter ridge on the lateral side. In the family Phasianidae, the latter ridge is not present in the genus *Phasianus* Linnaeus 1758, but it is well developed in the genera *Gallus* Brisson 1760 and *Pavo* Linnaeus 1758, where it separates groove 1 (for m. peroneus longus) from groove 2 (for m. flexor hallucis longus) (Ballman, 1969b:28, fig. 10). Between the internal and external ridges lies the groove for the tendons of m. flexor perforatus digiti 2 and m. flexor perforans and perforatus digiti 2 (groove 4), and behind this groove there is a roofed canal for the tendon of m. flexor digitorum longus. There is no noticeable difference between this hypotarsus and that of some Recent phasianids. A small, clearly projecting tubercle can be seen on the posterointernal angle of the proximal articular surface (Fig. 2t).

At the distal end, the internal trochlea is strongly projected posteriad, and it does not extend farther than the base of the middle trochlea. The external trochlea does not project laterad,

←

Figure 2. *Paraortyx lorteti:* right humerus, USTL, ITD 601, in palmar (**a**) and anconal (**b**) views, ×2; left coracoid, USTL, MGB 1547, in ventral (**c**) and dorsal (**d**) views, ×2; right ulna, USTL, ITD 564, in internal (**e**), palmar (**f**), and external (**g**) views, ×2; right scapula, proximal end, USTL, MGB 1554, in ventral (**h**) and dorsal (**i**) views, ×2; left carpometacarpus, MNHN Paris, QU 17131, in external (**j**) and internal (**k**) views, ×2; right carpometacarpus, internal (**l**) view, ×2 (arrow indicates the position of a small round tubercle on the os metacarpale minus); left tibiotarsus, MNHN Paris, QU 15684, in anterior (**m**) and posterior (**n**) views, ×2; left femur, MNHN Paris, QU 17003, in posterior (**o**) and anterior (**p**) views, ×2; left tarsometatarsus, MNHN Paris, QU 15865, in anterior (**q**) and posterior (**r**) views, the latter showing the well-preserved hypotarsus, ×2; right tarsometatarsus, USTL, ES 1, in anterior (**s**) and posterior (**t**) views, ×2 (the internal calcaneal ridge is broken).

Table 1. ***Paraortyx lorteti*** **and** ***Paraortyx brancoi:*** **Dimensions (mm) of the main long bones.**

	Paraortyx lorteti				*Paraortyx brancoi*			
	Mean	**Range**	**s**	**n**	**Mean**	**Range**	**s**	**n**
Coracoid								
Internal length	24.73	22.1–27.0	1.74	8	31.0	—	—	1
Width of cranial end (Fig. 4)	4.95	4.5–5.8	0.38	11	—	—	—	—
Width of midshaft	2.77	2.5–3.1	0.21	15	4.1	—	—	1
Depth of midshaft	2.11	1.9–2.7	0.23	15	2.6	—	—	1
Length of sternal facet	6.58	6.0–7.1	0.48	4	8.1 (est.)	—	—	1
Humerus								
Total length	39.96	37.0–42.6	1.53	10	50.45	49.6–51.3	1.20	2
Proximal width	10.31	9.2–11.2	0.61	15	12.50	12.2–12.9	0.36	3
Proximal depth	4.93	4.5–5.2	0.29	17	5.93	5.9–6.0	0.06	3
Distal width	7.91	7.2–8.7	0.42	20	9.63	9.5–9.9	0.19	4
Distal depth	4.16	3.7–4.7	0.27	21	5.17	5.0–5.3	0.15	3
Width of midshaft	3.46	3.0–4.0	0.27	17	4.04	3.8–4.2	0.17	5
Depth of midshaft	2.98	2.6–3.4	0.18	18	3.58	3.4–3.8	0.20	5
Ulna								
Total length	36.8	—	—	1	—	—	—	—
Proximal width	4.66	4.4–4.9	0.21	7	—	—	—	—
Proximal depth	6.23	5.7–6.6	0.34	6	—	—	—	—
Distal width	4.35	3.9–4.5	0.23	6	—	—	—	—
Depth of external condyle	4.25	4.1–4.5	0.14	6	—	—	—	—
Width of midshaft	2.22	2.1–2.4	0.12	6	—	—	—	—
Depth of midshaft	2.65	2.4–2.9	0.18	6	—	—	—	—
Carpometacarpus								
Total length	21.06	19.5–21.7	0.95	5	—	—	—	—
Proximal depth	6.69	6.1–7.0	0.26	8	—	—	—	—
Width of carpal trochlea	3.20	2.9–3.3	0.14	8	—	—	—	—
Width of metacarpale majus	2.50	2.1–2.7	0.20	7	—	—	—	—
Width of metacarpale minus	1.30	1.3–1.3	0	2	—	—	—	—
Distal depth	4.05	3.9–4.2	0.10	6	—	—	—	—
Distal width	2.42	2.1–2.5	0.16	6	—	—	—	—
Femur								
Total length	41.87	40.3–43.8	1.78	3	—	—	—	—
Proximal width	7.83	7.7–8.0	0.15	3	—	—	—	—
Proximal depth	4.95	4.9–5.0	0.07	2	—	—	—	—
Distal width	7.38	7.0–8.5	0.48	8	—	—	—	—
Distal depth	6.35	5.8–7.6	0.67	6	—	—	—	—
Width of midshaft	3.20	3.0–3.4	0.14	5	—	—	—	—
Depth of midshaft	3.08	2.8–3.4	0.22	5	—	—	—	—
Tibiotarsus								
Total length	52.0	—	—	1	—	—	—	—
Proximal width	6.17	5.9–6.5	0.31	3	—	—	—	—
Proximal depth	7.77	7.4–8.2	0.40	3	—	—	—	—
Distal width	5.66	5.6–5.8	0.08	7	—	—	—	—
Distal depth	5.77	5.5–6.1	0.24	7	—	—	—	—
Width of midshaft	3.05	2.9–3.2	0.21	2	—	—	—	—
Depth of midshaft	2.80	2.7–2.9	0.14	2	—	—	—	—
Tarsometatarsus								
Total length	33.48	29.3–36.8	3.01	6	45.0 (est.)*	—	—	1
Proximal width	5.85	5.5–6.3	0.34	9	8.0	—	—	1
Proximal depth	5.68	5.1–6.2	0.48	4	—	—	—	—
Distal width	6.48	6.1–7.3	0.35	12	—	—	—	—
Distal depth	4.78	4.3–5.8	0.46	10	—	—	—	—
Width of midshaft	2.77	2.5–3.0	0.16	10	4.3	—	—	1
Depth of midshaft	2.34	2.0–2.6	0.20	8	3.8	—	—	1

* Cast of a tarsometatarsus from the Museum of Munich, MGHN Lyon, PQ 1078.

although it extends distad distinctly farther than the internal trochlea and reaches to the center of the middle trochlea. The distal foramen is situated well proximal to the external intertrochlear notch. On the posterior surface, there is no depression, and the articular facet for the metatarsal I is not very marked. The differences between *Paraortyx* and *Palaeortyx* are that in *Paraortyx*, the external calcaneal ridge of the hypotarsus does not generally project so far posteriad as in the genus *Palaeortyx*, and groove 4 (for m. flex. pt. dig. 2 and m. p. and pt. dig. 2) is narrower and not clearly subdivided. At the distal end, in *Palaeortyx*, the internal trochlea is not so strongly projected posteriad but, rather, more projected mediad. The internal trochlea is also more elongated distad and extends halfway along the middle trochlea.

Figure 4. Method for measuring the width of the cranial end of coracoids of *Paraortyx*, *Quercymegapodius*, and *Palaeortyx*.

Paraortyx lorteti Gaillard 1908

Figure 2a–t

1892		*Palaeortyx cayluxensis* Milne-Edwards, p. 72.
1908	pars	*Palaeortyx cayluxensis* Lydekker: Gaillard, p. 100 (only humerus from Montauban).
1908		*Paraortyx Lorteti* Gaillard, p. 105, fig. 30, and pl. VI, figs. 5–8.
1933		*Palaeortyx Gaillardi* Lambrecht, p. 451.
1933		*Paraortyx Lorteti* Gaillard: Lambrecht, p. 456.
1964		*Ludiortyx gaillardi* (Lambrecht): Brodkorb, p. 299.
1964		*Paraortyx lorteti* Gaillard: Brodkorb, p. 299.

HOLOTYPE. Complete left humerus, Museum of Munich, no. 65. A cast of this humerus is stored in the collection of the MGHN Lyon, PQ 1083.

DIAGNOSIS. Smallest known species of the genus.

HORIZON AND LOCALITY. Upper Eocene to Lower Oligocene, Phosphorites du Quercy, France, Mammalian Standard Levels of Fons 4, Escamps, Soumaille, Villebramar and Itardies, MP (Mammalian Paleogene) 17, 19, 21, 22, and 23 (Schmidt-Kittler, 1987).

MATERIAL. New excavations: USTL Montpellier:

La Bouffie, Upper Eocene: left coracoids, cranial ends, BFI 1682, 1847; right tarsometatarsus, distal end, BFI 1758.

Perrière, Upper Eocene: left humerus, distal end and diaphysis, PRR 2587; almost complete right carpometacarpus, PRR 2589.

Escamps, Upper Eocene: almost complete left coracoid, ECC 3058.

Rosières 1 and **2,** Upper Eocene: left ulna, proximal end, ROS 1, 203; left ulna, distal end, ROS 1, 201; radius, distal end, ROS 2, 202; left femur, proximal end, ROS 2, 279; left tarsometatarsus, distal end, ROS 2, 204.

Ravet-Lupovici, Lower Oligocene: right humerus, distal end, RAV 79.

Mas de Got B, Lower Oligocene: complete left coracoid, MGB 1547; right coracoid, cranial end, MGB 1560; right scapula, anterior end, MGB 1554; left scapula, anterior end, MGB 1557; right tarsometatarsus, proximal end, MGB 1549.

Itardies, Lower Oligocene: 2 almost complete right coracoids, ITD 530, 624; 2 right coracoids, cranial ends, ITD 554, 694; right coracoid, sternal end, ITD 681; 2 almost complete left coracoids, ITD 636, 637; 3 cranial ends of left coracoids, ITD 574, 711, 725; central part of furcula, ITD 558; complete right humerus, ITD 601; almost complete right humerus, ITD 604; 3 right humeri, proximal ends, ITD 615, 630, 659; 2 left humeri, proximal ends, ITD 531, 608; 4 left humeri, distal ends, ITD 633, 657, 660, 661; complete left ulna, ITD 564; 2 right ulnae, proximal ends, ITD 646, 677; 2 right ulnae, distal ends, ITD 534, 557; left ulna, proximal end, ITD 680; left ulna, distal end, ITD 651; radius, distal end, ITD 536; complete right carpometacarpus, ITD 566; right carpometacarpus, proximal end, ITD 692; left carpometacarpus, proximal end, ITD 654; 6 right femora, distal ends, ITD 525, 549, 550, 596, 650, 672; left femur, proximal end, ITD 529; 2 left femora, distal ends, ITD 535, 552; right tibiotarsus, proximal end, ITD 613; 2 right tibiotarsi, distal ends, ITD 571, 584; left tibiotarsus, proximal part, ITD 706; 4 left tibiotarsi, distal ends, ITD 572, 668, 697, 699; 2 right tarsometatarsi, proximal ends, ITD 669, 690; 4 right tarsometatarsi, distal ends, ITD 528, 567, 652, 698; almost complete left tarsometatarsus, ITD 602; left tarsometatarsus, proximal end, ITD 537; 4 left tarsometatarsi, distal ends, ITD 532, 635, 685, 689; phalanx 1 of posterior digit II, ITD 713; plus several elements from the same individual—complete right coracoid, proximal end of left humerus, distal end of left ulna, proximal end of radius, distal end of radius, central part of furcula, distal end of right tarsometatarsus, ITD 577.

Roqueprune 2, Lower Oligocene: complete right humerus, ROQ 91; right humerus, diaphysis, ROQ 305; left humerus, distal end, ROQ 308; left coracoid, sternal end, ROQ 309; right ulna, proximal end, ROQ 316.

Early Collections without Provenance. MNHN Paris: 4 almost complete right humeri, QU 15531, 15533, 15589, 15596; right humerus, proximal end, QU 15581 (holotype of the species *Palaeortyx cayluxensis* Milne-Edwards); 4 almost complete left humeri, QU 15574, 15583, 15588, 16933; left humerus, distal end, QU 15576; almost complete right carpometacarpus, QU 15885; complete left carpometacarpus, QU 17131; 3 almost complete right femora, QU 15685, 17026, 17029; almost complete left femur, QU 17003; almost complete left tibiotarsus, QU 15684; almost complete right tarsometatarsus, QU 16968; almost complete left tarsometatarsus, QU 15865. MGHN Lyon: Cast of the holotype left humerus, no. 65, Museum of Munich, PQ 1083; cast of a complete right humerus from the Museum of Montauban, PQ 1066. MHN Montauban: Incomplete left humerus, MA 39. MNH Basel: 3 almost complete left coracoids, Q.D. 548, Q.H. 773, Q.N. 194; complete right tarsometatarsus, juvenile, Q.W. 513.

MEASUREMENTS. See Table 1.

REMARKS. The species *Paraortyx lorteti* extends over a temporal range of seven mammalian standard-levels, or at least 7 million years. Nonetheless, it is not possible to detect any temporal change in size. Individual size variation within this

species is considerable (Table 1) and may be attributable to sexual dimorphism.

Paraortyx brancoi Gaillard 1908

Figure 5a–d

1908		*Paraortyx Brancoi* Gaillard, p. 107, fig. 31, and pl. VI, figs. 9–16.
1933		*Paraortyx Brancoi* Gaillard: Lambrecht, p. 456.
1939	non	*Paraortyx Brancoi* Gaillard: Gaillard, p. 24, fig. 11.
1964		*Paraortyx brancoi* Gaillard: Brodkorb, p. 300.
1978		*Paraortyx brancoi* Gaillard: Mourer-Chauviré, p. 219, pl. 1, figs. 1, 2.

HOLOTYPE. Complete left humerus, Museum of Berlin. A cast of this humerus is stored in the collection of the MGNH Lyon, PQ 1078.

EMENDED DIAGNOSIS. Largest known species of the genus.

HORIZON AND LOCALITY. Upper Eocene, Phosphorites du Quercy, France. Standard Levels of La Débruge and Escamps, MP 18 and 19 (Schmidt-Kittler, 1987).

MATERIAL. New excavations: USTL Montpellier:

Sainte-Néboule, Upper Eocene: right humerus, distal end and diaphysis, SNB 703.

Escamps, Upper Eocene: almost complete right coracoid, ECC 3216; right humerus, fragment of proximal end, ECC 3053.

Rosières 2, Upper Eocene: anterior part of furcula, ROS 2 280.

Early Collections without Provenance. MNHN Paris: Right humerus, proximal end and diaphysis, QU 16918; right humerus, proximal end, from a site called "Sindou Brunet"; almost complete left humerus, QU 17146; incomplete left humerus, QU 16917. MGHN Lyon: Cast of the holotype left humerus from the Museum of Berlin, PQ 1078; cast of an incomplete left tarsometatarsus, no. 119, Museum of Munich, PQ 1078.

MEASUREMENTS. See Table 1.

REMARKS. In 1939, Gaillard attributed two femora from the MNH Basel collection to the species *Paraortyx brancoi* (Q.N. 492 and Q.D. 678; femur Q.N. 492 is illustrated in Gaillard, 1939:25, fig. 11). These two bones belong to the species *Elaphrocnemus phasianus* Milne-Edwards 1892 (Mourer-Chauviré, 1983:93). Gaillard also attributed a pelvis, Q.N. 141, to *P. brancoi,* but it is not possible to affirm that it actually belongs to the genus *Paraortyx* (Gaillard, 1939:26, fig. 12).

DESCRIPTION AND COMPARISONS. The diagnosis given by Gaillard (1908:107) is as follows [my translation]: "Humerus resembling that of *Paraortyx lorteti* by its main features, but humeral head higher, pectoral crest [=deltoid crest] more internally curved, insertion surface of the great pectoral [attachment of the m. pectoralis; Ballmann, 1969b] more elongated. In addition, the attachment of the middle pectoral [pectoral attachment of Howard (1929) or attachment of the m. supracoracoideus of Ballmann (1969b)] extends much less downward. Seen in profile, humerus more curved than that of *P. lorteti.* Distal part well developed, with tricipital groove rather deep because of the extensive projection of the epitrochlea [entepicondyle]. On the anterior face, the impression of m. brachialis anticus is long and well pronounced."

When comparing a series of humeri of *Paraortyx lorteti* with those of *P. brancoi,* it is clear that the humeral head of the latter is proportionally more globular and the attachment of m. supracoracoideus proportionally shorter. On the other hand, the humerus of *P. brancoi,* seen in profile, is not more curved than that of *P. lorteti,* its deltoid crest is not more internally curved, and the attachment of m. pectoralis is not more elongated. The main difference between these two forms is their size (Table 1).

The coracoid does not have any distinctive features except for its large size. Gaillard (1908) attributed an incomplete left tarsometatarsus from the Munich Museum to *Paraortyx brancoi.* The hypotarsus is incompletely preserved and the middle and internal trochleae are missing. However, from what can be seen of the hypotarsus, there is no difference between it and that of *P. lorteti.* Also, the ratios between the dimensions of the tarsometatarsus of this specimen compared to those of *P. lorteti* are almost the same as the ratios between the dimensions of the humeri and coracoids of *P. brancoi* compared to those of *P. lorteti.* Therefore, this specimen seems to be correctly attributed to *P. brancoi.*

Pirortyx Brodkorb 1964

1939	pars	*Palaeortyx* Milne-Edwards: Gaillard, p. 21.
1964		*Pirortyx* Brodkorb, p. 300.

TYPE SPECIES. *Pirortyx major* (Gaillard 1908).

INCLUDED SPECIES. Type species only.

ORIGINAL DIAGNOSIS. "Head of humerus very wide transversely, compressed in anterior–posterior direction. Subtrochanteric fossa large but shallower than in *Palaeortyx* and pierced by a pneumatic foramen (lacking in *Palaeortyx*). Angle of deltoid crest proximal to level of internal tuberosity (below level in *Palaeortyx*). Shaft stout, strongly curved in lateral view. Entepicondyle short" (Brodkorb, 1964:300).

EMENDED DIAGNOSIS. Humerus with wide, but shallow, tricipital fossa. Humeral head not connected by a ridge to the internal tuberosity, so that the capital groove communicates with the tricipital fossa, as in the genus *Paraortyx.* Deep pneumatic fossa, pierced by a large pneumatic foramen.

DISTRIBUTION. Upper Oligocene, Phosphorites du Quercy, France.

REMARKS. I do not agree with the sentence in the original diagnosis: "Angle of deltoid crest proximal to level of internal tuberosity (below level in *Palaeortyx*)." This feature is the result of an optical illusion when using Gaillard's illustrations. In fact, the humeri of both *Pirortyx* and *Palaeortyx* have the angle of the deltoid crest situated practically at the same level as the internal tuberosity.

Pirortyx major (Gaillard 1939)

Figure 5e–g

1939	*Palaeortyx major* Gaillard, p. 22, fig. 10.
1964	*Pirortyx major* (Gaillard): Brodkorb, p. 300.

HOLOTYPE. Almost complete right humerus, collection of the MNHN Paris, QU 16297.

DIAGNOSIS. As for genus.

MEASUREMENTS (mm) OF HOLOTYPE. Total length, 56.4; proximal width, 14.4; proximal depth, 7.1; distal width, 9.7; distal depth, 5.6; midshaft width, 5.0; midshaft depth, 4.2.

HORIZON AND LOCALITY. Upper Oligocene, Phosphorites du Quercy, France.

MATERIAL. New excavations: MNHN Paris:

Pech du Fraysse, Upper Oligocene: left humerus, proximal end, PFR 11002. Measurements (mm): Proximal width, 13.5;

proximal depth, 6.8 (est.); midshaft width, 4.9; midshaft depth, 4.1.

Early Collections without Provenance. MNHN Paris: Holotype.

DESCRIPTION AND COMPARISONS. The genus *Pirortyx* differs from *Paraortyx* in that its tricipital fossa is shallow, whereas in *Paraortyx* it is deep and extends under the humeral head, and because its pneumatic fossa is pierced by a large pneumatic foramen, which is absent in *Paraortyx*. I include it in the family Paraortygidae because, as in *Paraortyx* and unlike what is found in all Recent galliforms, the humeral head is not connected by a ridge to the internal tuberosity (Fig. 6). Distally, the entepicondyle is not very well preserved, but it seems less protrudent than that of *Paraortyx*. *Pirortyx* is very rare in the Phosphorites du Quercy, being represented by only two specimens.

COMPARISON OF THE PARAORTYGIDAE WITH THE OTHER FOSSIL FORMS

GALLINULOIDIDAE. This family includes the genera *Gallinuloides* Eastman, from the Lower Eocene (and not Middle Eocene) of Wyoming (Savage and Russell, 1983), *Procrax* Tordoff and Macdonald, from the Lower Oligocene of South Dakota, and *Taoperdix* Milne-Edwards, from the end of the Lower Oligocene of Armissan (France). These genera are represented by almost complete skeletons, on slabs. A ratio-diagram (Simpson, 1941) (Fig. 7) shows that the Paraortygidae differ from the Gallinuloididae by the proportions of the different parts of the skeleton. The ulna, the carpometacarpus, and the tibiotarsus are proportionally much more elongated in the Gallinuloididae. This diagram also shows that the proportions of the main long bones of the Gallinuloididae are very similar to those of some Recent Cracidae, e.g., *Crax rubra* Linnaeus 1758, and differ from those of the Recent Phasianinae, i.e., *Perdix perdix* Linnaeus 1758. On the impressions of the skeletons of the species of the Gallinuloididae, it is not possible to see the shape of the scapular facet of the coracoid or the proximal part of the humerus; however, it is possible to see that the intermetacarpal process is absent on the carpometacarpus. The coracoid of *Gallinuloides* is relatively short and stout and its sternal facet is considerably arched (Eastman, 1900), whereas the coracoids of *Paraortyx* are proportionally more elongated and their sternal facet weakly arched.

PHASIANIDAE. Harrison and Walker (1977, 1979a, 1979b) described in the Phasianidae the genera *Argillipes*, *Percolinus*, *Coturnipes*, and *Litoripes*. *Argillipes* is found from the Lower Eocene to the Lower Oligocene of England, *Percolinus* from the Lower to the Middle Eocene, *Coturnipes* in the Lower Eocene, and *Litoripes* in the Middle Eocene. In all of these genera, the tarsometatarsus is the only known bone, except for *Argillipes aurorum*, for which Harrison and Walker (1977) have also reported the distal end of a humerus. Neither the coracoid, nor the proximal part of the humerus, nor the carpometacarpus are known; therefore, it is difficult to ascertain whether these forms actually belong to the Phasianidae, or could be attributed to the Paraortygidae. In *Argillipes*, the hypotarsus is small and weakly projecting posteriad and, thus, differs from that of *Paraortyx*. For *Litoripes medius*, an almost complete tarsometatarsus is known, and it resembles that of *Paraortyx lorteti* in size but differs from it by the lesser width of its distal end.

Weigel (1963) described the species *Nanortyx inexpectatus* from the lowermost Chadronian of Cypress Hills, Saskatchewan. This species was placed in the Phasianidae, subfamily Odontophorinae, by Brodkorb (1964). The Chadronian corresponds to the end of the Eocene and the Lower Oligocene (Savage and Russell, 1983); thus, it seems that *Nanortyx* may be the same age as the forms from the Upper Eocene of Quercy. The holotype is a distal end of a tarsometatarsus. The coracoid that is referred to the same species seems to have a hollow scapular facet, as in *Paraortyx*, but this is not precisely stated in the description. It differs, however, from *Paraortyx* in having an intermuscular line weakly indicated and a shaft that is circular in cross-section.

Quercymegapodiidae new family

TYPE GENUS. *Quercymegapodius* new genus.

DIAGNOSIS. Humerus with a swollen head, tricipital fossa slightly marked, pneumatic fossa wide and shallow, closed by a very thin bony blade pierced by several small pneumatic foramina; longitudinal ridge on the proximal part of the anconal surface, in the prolongation of the internal side of the tricipital fossa. Coracoid with a concave scapular facet. Carpometacarpus with an extremely poorly developed intermetacarpal process, and a small, hook-like, distally incurved apophysis on the internal face of metacarpale minus. Tarsometatarsus with internal and external trochleae strongly divergent and internal trochlea shorter than the external one.

INCLUDED GENERA. Type genus only.

TEMPORAL AND GEOGRAPHIC DISTRIBUTION. Upper Eocene, Phosphorites du Quercy; and Lower Miocene, Saint-Gérand-le-Puy (France).

Quercymegapodius new genus

1908		*Palaeocryptonyx* Depéret: Gaillard, p. 95.
1933		*Palaeocryptonyx* Depéret: Lambrecht, p. 437.
1964	pars	*Pirortyx* Brodkorb, p. 300.
1978		Galliforme, genre et espèce inconnus: Mourer-Chauviré, p. 220, pl. 1, figs. 3, 4.

TYPE SPECIES. *Quercymegapodius depereti* (Gaillard 1908).

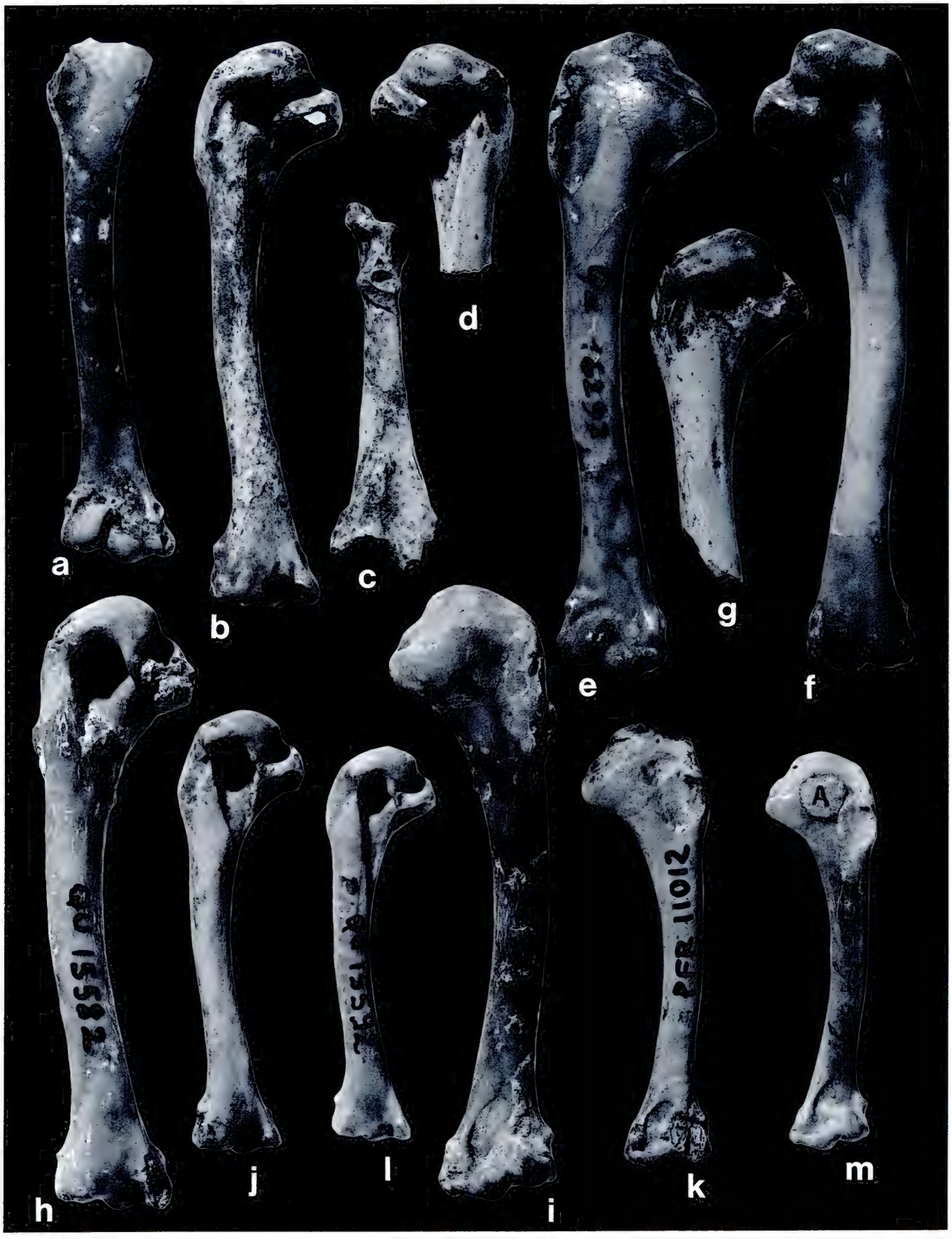
DIAGNOSIS. As for family.

INCLUDED SPECIES. Type species; *Quercymegapodius brodkorbi* new species.

DISTRIBUTION. Upper Eocene, Phosphorites du Quercy, France.

ETYMOLOGY. From the name of the old province of Quercy and *Megapodius*, generic name for one group of mound builders.

BACKGROUND. Gaillard (1908) placed this form in the genus *Palaeocryptonyx* Depéret (1892), which was established for a small galliform from the Pliocene of Perpignan, France. However, the Quercy form has a weakly indicated tricipital fossa, whereas the one from Perpignan has a very deep tricipital fossa that penetrates under the humeral head. Brodkorb (1964) established the genus *Pirortyx*, in which he placed the species *Pirortyx major* (Gaillard 1939) and *Palaeocryptonyx depereti* Gaillard 1908, the type species being *Pirortyx major*. In fact, in *Pirortyx major*, the tricipital fossa is wide and shallow and the pneumatic fossa is very deep and has a large pneumatic foramen. In *Palaeocryptonyx depereti*, the tricipital fossa is weakly indicated and the pneumatic fossa shallow. Moreover, the bottom of this fossa is occupied by a very thin bony blade, pierced by several small foramina. For these reasons, it is not possible to maintain the species *Palaeocryptonyx depereti* in the genus *Pirortyx*. Because I assign this species to a different family, it is necessary to establish a new generic name for it.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DESCRIPTIONS AND COMPARISONS. 1. Comparison with Recent Forms. The living megapodes include seven genera that are found principally east of the Wallace line, in the Philippines, the Moluccas, the Celebes, New Guinea, Australia, and the New Hebrides. The comparative material that I had the opportunity to study includes complete skeletons of the Recent genera *Megapodius* Gaimard 1823, *Macrocephalon* S. Müller 1846, *Eulipoa* Ogilvie-Grant 1893, *Alectura* Latham 1824, and *Leipoa* Gould 1840 and partial skeletons of *Tallegalla* Lesson 1828 and *Aepypodius* Oustalet 1880.

Humerus (Figs. 1b, c, f, g, r, s, 8): In Recent megapodes, the humeral head is proximodistally elongated, especially in *Alectura*. The tricipital fossa is rudimentary. The anconal face of the bone, at its proximal end, has a longitudinal ridge (capital shaft ridge; Ashley, 1941), situated along its main axis, most conspicuously in *Megapodius, Eulipoa,* and *Alectura*. The development of this ridge can be correlated with the fact that the m. latissimus dorsi attachment, which is situated on the internal side of the shaft, below the pneumatic fossa, in all extant galliforms (including the Cracidae), is here (in Recent megapodes) on the external side, in the shape of a thin, elongated line. The pneumatic fossa is very shallow, and it is closed by a thin bony blade perforated by very small pneumatic foramina in *Megapodius, Eulipoa,* and *Alectura*. It is a little deeper with larger foramina in *Macrocephalon* and *Leipoa*.

On the palmar face, the deltoid crest is strongly widened at its base and not very protrudent. The bicipital surface and the bicipital furrow are not clearly differentiated and form a rather flattened area. The ligamental furrow is very short, shallow, and restricted to the internal side.

Most of these features can be found in the Quercy forms; however, they look more similar to *Megapodius* and *Eulipoa* spp. because, in these genera, the longitudinal ridge of the anconal face is more conspicuous, the humeral head is relatively less proximodistally elongated, and the pneumatic fossa is shallower than that of the other examined genera of Megapodiidae (Fig. 8).

The differences between the humerus of *Quercymegapodius* and that of Recent megapodes are as follows. In *Quercymegapodius,* the humeral head forms a rim above the capital groove; this rim is less pronounced in megapodes. In megapodes, the humeral head is connected to the internal tuberosity by a small ridge that interrupts the capital groove and separates it from the tricipital fossa; in *Quercymegapodius* this ridge does not exist on specimen MA 5 (Fig. 1f), and it is very rudimentary on the other specimens (Fig. 1b, r). As already stated, the weak development or the absence of this ridge can be considered a primitive character. In *Quercymegapodius,* the pneumatic fossa is relatively more conspicuous, the deltoid crest is thinner at its base and more projecting, and, at the distal end, the external condyle is more vertically inclined than in megapodes.

Coracoid (Fig. 1d, e, t, u): I have ascribed to the genus *Quercymegapodius* coracoids that show a concave scapular facet similar to that in *Paraortyx,* and some other characters similar to those of Recent megapodes. This type of coracoid is also found in the Lower Miocene deposits of Saint-Gérand-le-Puy, where it can be associated with humeri related to Megapodiidae.

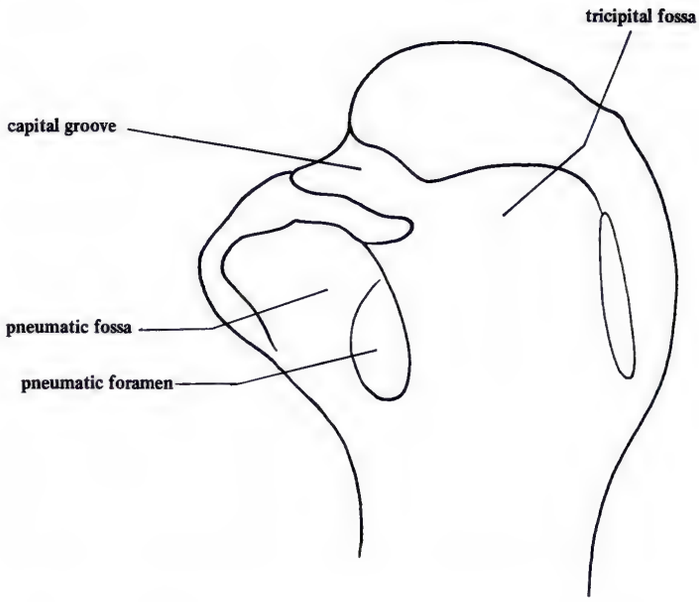


Figure 6. Drawing of the proximal end of the humerus, anconal view, of the genus *Pirortyx*.

The features in common with Recent megapodes are as follows: The scapular facet has a rounded shape; below this facet, the shaft is relatively narrow and the internal and external sides are almost parallel; the shaft widens only at some distance from the scapular facet, and it is circular in cross-section. The Quercy forms resemble *Megapodius* and *Eulipoa* spp. in that they have a well-developed glenoid facet, projecting on the external side, and an acrocoracoid that is more curved caudally. However, the coracoids attributed to *Quercymegapodius* spp. differ from those of species of the Recent family Megapodiidae because the latter have a rounded convex scapular facet instead of a rounded concave one. The concave scapular facet is a primitive character.

Carpometacarpus (Figs. 1l–q, 9): In Recent megapodes, the metacarpale minus is very thin in the genera *Megapodius, Eulipoa, Alectura,* and *Macrocephalon*. It diverges strongly from the metacarpale majus in *Alectura* and *Macrocephalon,* less so in *Megapodius, Eulipoa,* and *Leipoa*. The intermetacarpal apophysis is only slightly marked in the five examined genera. On the internal face of the metacarpale minus, near its proximal fusion with the metacarpale majus, there is a small, hook-like apophysis, which is curved distally. This apophysis is conspicuous in *Megapodius* and *Eulipoa,* rudimentary in *Macrocephalus* and *Leipoa,* and absent in *Alectura* (Fig. 9). Within the Recent

←

Figure 5. *Paraortyx brancoi:* right humerus, USTL, SNB 703, in palmar (**a**) view, ×2; almost complete left humerus, MNHN Paris, QU 17146, in anconal (**b**) view, ×2; almost complete right coracoid, USTL, ECC 3216, in dorsal (**c**) view, ×2; right humerus, proximal end, MNHN Paris, "Sindou Brunet," in anconal (**d**) view, ×2. *Pirortyx major:* holotype right humerus, MNHN Paris, QU 16297, in palmar (**e**) and anconal (**f**) views, ×2; left humerus, proximal end, MNHN Paris, PFR 11002, in anconal (**g**) view, ×2. *Palaeortyx intermedia:* left humerus, MNHN Paris, QU 15582, in anconal (**h**) and palmar (**i**) views, ×2. *Palaeortyx gallica:* left humerus, MNHN Paris, PFR 11012, in anconal (**j**) and palmar (**k**) views, ×2. *Palaeortyx brevipes:* left humerus MNHN Paris, QU 15592, in anconal (**l**) and palmar (**m**) views, ×2.

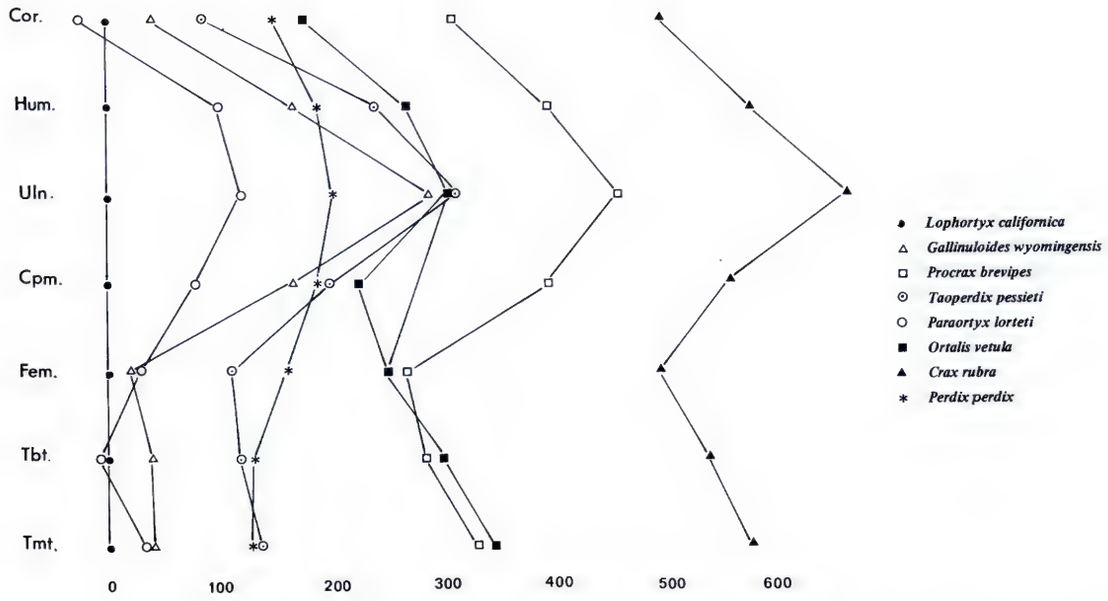


Figure 7. Simpson's (1941) ratio-diagram of the log differences of the main long bones in the fossil family Gallinuloididae (*Gallinuloides wyomingensis* and *Procrax brevipes*, measurements of Tordoff and Macdonald, 1957; *Taoperdix pessieti*, measurements of Eastman, 1905, for the Carnegie Museum specimen), in the fossil family Paraortycidae (*Paraortyx lorteti*, mean dimensions; Table 1), in some Recent Cracidae (*Ortalis vetula* and *Crax rubra*), and in a Recent Phasianinae (*Perdix perdix*). The Recent *Lophortyx californica* has been taken as standard.

genera, the process of the alular metacarpal projects proximad considerably in *Megapodius*, *Eulipoa*, and *Macrocephalon*, not so much in *Alectura*, and only slightly in *Leipoa*. It ends in a rounded, tubercle-like knob in *Alectura*, *Macrocephalon*, and *Leipoa*, but it is less swollen in *Megapodius* and *Eulipoa*. The pisiform process projects strongly in *Alectura*, less in *Megapodius*, *Eulipoa*, and *Macrocephalon*, and it is flattened in *Leipoa*. There is no fossa on the internal side of the process of the alular metacarpal (depressio muscularis interna; Ballmann 1969b) in *Alectura* and *Megapodius*, but this fossa is present, albeit only slightly developed, in *Macrocephalon* and *Leipoa*.

On the posterior face, the external edge of the carpal trochlea is much shorter than the internal edge in *Alectura* and *Leipoa*, whereas it is longer in *Megapodius* and *Macrocephalon*. In proportion to the length of the bone, the shaft of the metacarpale majus is much thinner in *Megapodius* and *Eulipoa* than in the other three examined genera. The articular facet for the digitus minor is situated lower than the facet for the digitus major in *Alectura*, *Macrocephalon*, and *Leipoa*, whereas the step between the two facets is weaker in *Megapodius* and *Eulipoa*.

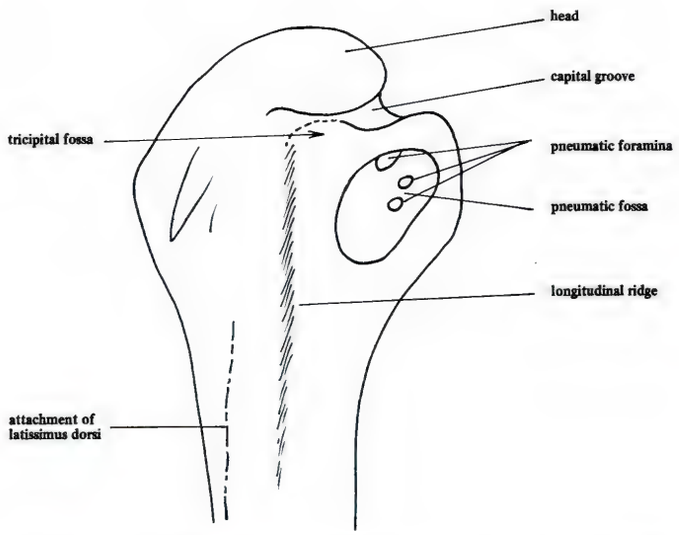


Figure 8. Drawing of the proximal end of the humerus, anconal view, of the genus *Quercymegapodius*.

The carpometacarpus of *Quercymegapodius* is similar to that of Recent *Megapodius* and *Eulipoa* spp. in the following characteristics: very thin metacarpale minus; relatively slender metacarpale majus; alular metacarpal thin, projecting strongly proximad, and not very swollen at its end; intermetacarpal apophysis only slightly marked; small hook-like apophysis on the internal face of the metacarpale majus; depressio muscularis interna absent; on the posterior face, external edge of the carpal trochlea extending as far as the internal edge (Fig. 9); on the distal end, articular facet for the digitus minor situated almost at the same level as the facet for the digitus major.

The differences among the genera *Quercymegapodius*, *Megapodius*, and *Eulipoa* are as follows: On the posterior face in *Megapodius*, the metacarpale minus is fused, at its proximal end, on the internal face of the metacarpale majus, whereas in *Eulipoa* and *Quercymegapodius* it is fused more along the axis of the metacarpale majus; at the distal end, the articular facets for the digiti major and minor are situated almost in the same plane in the Quercy form, whereas there is a small step between them in *Megapodius* and *Eulipoa*.

Tibiotarsus. I have attributed to *Quercymegapodius* a distal end of a tibiotarsus. In most Recent megapodes (except in *Aepypodius*), this part is very different from that of the other galliforms in that it is transversally flattened, the two condyles are broad and flat, the intercondylar groove is broad and shallow, and the articular surface of the external condyle extends proximad and continues onto the external part of the supratendinal bridge.

The distal end of the tibiotarsus of *Quercymegapodius* differs from that of *Megapodius* and *Eulipoa* in that it is not as flattened transversally, but the intercondylar groove is broad and the external condyle continues onto the external part of the supratendinal bridge as in the extant genera.

Tarsometatarsus (Fig. 1h–k). In extant megapodes, the hypotarsus shows a very broad canal, circular or oval in shape, and three ridges: a large internal one and two external ones. These ridges separate four grooves: a very broad internal groove, a median groove (groove 4 of Ballmann, 1969b), and two external grooves (grooves 1 and 2 of Ballmann, 1969b). The internal ridge projects strongly posteriad in *Megapodius* and *Eulipoa*. The shaft of the bone is much deeper on the external side compared to the internal side. In *Alectura, Macrocephalon, Aepypodius,* and *Talegalla,* on the internal side of the proximal end, the shaft is reduced to a blade, as in the family Cracidae, but the reduction is not so marked in *Megapodius, Eulipoa,* and *Leipoa.*

In *Alectura, Macrocephalon, Leipoa, Aepypodius,* and *Talegalla,* the internal trochlea projects strongly mediad, as in the family Cracidae, whereas the distal end is more symmetrical in *Megapodius* and *Eulipoa,* where the external and internal trochleae diverge widely, as it can be seen, for example, in the Otididae. In the five former genera, the shaft widens progressively toward the distal end; in *Megapodius* and *Eulipoa,* the shaft is straighter and widens abruptly at the level of the trochleae; the external trochlea projects farther externad than in other galliforms, and a well-marked articular groove runs along it. In the other genera, the articular groove on the external trochlea is much less marked.

In most Recent megapodes that I have examined, the internal trochlea extends a little farther distad than the external trochlea, and it is conspicuously shorter than the middle trochlea. But in *Aepypodius,* the external and internal trochleae extend at the same level. However, the relative length of the internal and external trochleae may be subject to individual variation because Holman (1964) indicates that the internal trochlea is longer than the external trochlea in *Alectura* and *Leipoa,* whereas they are the same length in *Megapodius* and *Macrocephalon.* The distal foramen is large, open, and situated very close to the intertrochlear notch.

The tarsometatarsi of *Quercymegapodius* are more different from those of *Megapodius* or *Eulipoa* than are the humeri and carpometacarpi. The common characteristics are as follows: The internal and external trochleae are much more divergent than in other galliforms; the internal trochlea is globular in shape and shows no articular groove; the distal foramen is large, open, and situated just above the intertrochlear notch. *Quercymegapodius* differs from *Megapodius* and *Eulipoa* in having its internal hypotarsal ridge not projecting as far posteriad. On specimen QU 15869, the internal trochlea is conspicuously shorter than the external trochlea, unlike what can be found in extant megapodes (Fig. 1h, i). On specimen QU 16973, the internal trochlea is slightly shorter than the external trochlea, but the difference in length between the two trochleae is much smaller (Fig. 1j, k). On the external trochlea of this specimen, the articular groove is only slightly marked. Finally, the ratio between the length of the tarsometatarsus and the length of the humerus is smaller: In *Quercymegapodius,* the length of the tarsometatarsus averages 75 percent of that of the humerus, whereas it reaches 86 percent in *Megapodius.*

2. Comparison with Fossil Forms. The family Megapodiidae is as yet unknown in the Tertiary. In the Quaternary, several large extinct forms have been reported from Australia (Van Tets, 1974) and from New Caledonia (Poplin and Mourer-Chauviré, 1985).

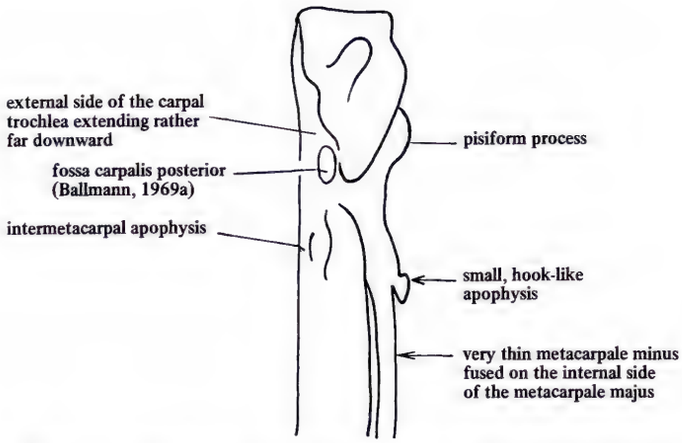

external side of the carpal trochlea extending rather far downward
fossa carpalis posterior (Ballmann, 1969a)
intermetacarpal apophysis
pisiform process
small, hook-like apophysis
very thin metacarpale minus fused on the internal side of the metacarpale majus

Figure 9. Drawing of the proximal part of the carpometacarpus, posterior view, in the Recent genus *Megapodius.*

The humeri of the family Quercymegapodiidae resembles that of the family Paraortygidae by the slight development of the ridge that connects the humeral head to the internal tuberosity, this ridge being absent in the Paraortygidae, but they differ by the shallowness of their tricipital and pneumatic fossae.

The coracoids attributed to the genus *Quercymegapodius* have, as do those of *Paraortyx,* a concave scapular facet. However, they differ because in *Paraortyx* the scapular facet is obliquely elongated relative to the long axis of the shaft (Fig. 2d), whereas it is circular in *Quercymegapodius* (Fig. 1e, u). Moreover, in *Quercymegapodius,* the procoracoid is completely missing. In *Paraortyx,* below the procoracoid, there is an intermuscular line that follows the posterointernal border of the shaft in describing an arc (Fig. 2d); this line does not exist in *Quercymegapodius* (Fig. 1e, u). Below the scapular facet, the internal and external sides are divergent in *Paraortyx,* whereas they are almost parallel in *Quercymegapodius.* The shaft is flattened on its posterior face in *Paraortyx* but not in *Quercymegapodius.* In *Quercymegapodius,* the cross-section of the shaft is proportionally narrow relative to the head of the coracoid and the glenoid facet is well developed and projects externad. The ratio between the width of the cranial end and the width of the shaft is higher than 2 in *Quercymegapodius* (mean = 2.31; n = 2), whereas it is always lower than 2 in *Paraortyx* (*P. lorteti,* mean = 1.85; n = 8). On the ventral face, the acrocoracoid is more strongly recurved caudad in *Quercymegapodius* than in *Paraortyx.*

In general appearances, the coracoid attributed to *Nanoptyx inexpectatus* Weigel 1963 resembles the Quercymegapodiidae more than the Phasianidae. However, it differs from *Quercymegapodius* in that its procoracoid is rather marked and its glenoid facet does not project so much on the external side.

Quercymegapodius depereti (Gaillard 1908)

Figure 1b–m

1908 *Palaeocryptonyx Depereti* Gaillard, p. 96, fig. 26, and pl. V, figs. 9–12.

1933 *Palaeocryptonyx Depereti* Gaillard: Lambrecht, p. 437.

Table 2. *Quercymegapodius depereti* and *Quercymegapodius brodkorbi* n. sp.: Dimensions (mm) of the long bones.

	Quercymegapodius depereti				*Quercymegapodius brodkorbi*			
	Mean	Range	s	n	Mean	Range	s	n
Humerus								
Total length	40.00	39.7–40.4	0.29	4	—	—	—	—
Proximal width	9.73	9.5–9.9	0.17	4	8.2	—	—	1
Proximal depth	4.97	4.9–5.0	0.06	3	4.0	—	—	1
Distal width	7.52	7.0–7.7	0.29	5	5.75	5.7–c. 5.8	0.07	2
Distal depth	3.92	3.6–4.1	0.19	5	3.1	—	—	1
Width of midshaft	3.40	3.3–3.5	0.08	4	2.40	2.4–2.4	0	2
Depth of midshaft	2.93	2.9–3.0	0.05	4	2.15	2.0–2.3	0.21	2
Coracoid								
Width of cranial end (Fig. 4)	5.4	—	—	1	3.80	3.5–4.1	0.42	2
Width of midshaft	2.2	—	—	1	1.9	—	—	1
Depth of midshaft	1.8	—	—	1	1.5	—	—	1
Carpometacarpus								
Total length	22.5	—	—	1	19.60	19.4–19.8	0.28	2
Proximal depth	5.9	—	—	1	5.35	5.1–5.6	0.35	2
Width of carpal trochlea	3.0	—	—	1	2.75	2.7–2.8	0.07	2
Width of metacarpale majus	2.2	—	—	1	2.05	1.9–2.2	0.21	2
Width of metacarpale minus	0.9	—	—	1	0.9	—	—	1
Distal depth	4.2	—	—	1	3.2	—	—	1
Distal width	2.3	—	—	1	1.95	1.9–2.0	0.07	2
Tibiotarsus								
Distal width	—	—	—	—	4.7	—	—	1
Distal depth	—	—	—	—	4.7	—	—	1
Tarsometatarsus								
Total length	30.0	—	—	1	—	—	—	—
Distal width	5.80	5.5–6.1	0.42	2	—	—	—	—
Distal depth	3.75	c. 3.6–3.9	0.21	2	—	—	—	—
Width of midshaft	2.50	2.4–2.6	0.14	2	—	—	—	—
Depth of midshaft	1.70	1.7–1.7	0	2	—	—	—	—

1964 *Pirortyx depereti* (Gaillard): Brodkorb, p. 300.
1978 Galliforme, genre et espèce inconnus: Mourer-Chauviré, p. 220, pl. 1, figs. 3, 4.

HOLOTYPE. Complete left humerus, collection of the Munich Museum, no. 127. A cast of this humerus is in the collection of the MGHN Lyon, PQ 1065.

DIAGNOSIS. Humerus with pneumatic fossa very shallow. Largest species in the genus.

HORIZON AND LOCALITY. Upper Eocene, Phosphorites du Quercy, France.

MATERIAL. New excavations: USTL Montpellier:

Sainte-Néboule, Upper Eocene: right coracoid, cranial end and diaphysis, SNB 700.

Escamps, Upper Eocene: almost complete left humerus, ECC 3060; left humerus, distal end, ECA 3206.

Early Collections without Provenance. MNHN Paris: Almost complete left humerus, QU 16932; complete left tarsometatarsus, QU 15673; almost complete right tarsometatarsus, QU 15869; right tarsometatarsus, distal end and diaphysis, QU 16973. MGHN Lyon: Cast of the holotype left humerus (no. 127 of the Munich Museum), PQ 1065. MHN Montauban: Complete right humerus, MA 5.

MEASUREMENTS. See Table 2.

Quercymegapodius brodkorbi new species

Figure 1n–u

HOLOTYPE. Almost complete left carpometacarpus, collection USTL Montpellier, site of Rosières 1, ROS 1, 202.

DIAGNOSIS. Humerus with a swollen head, tricipital fossa slightly marked, pneumatic fossa deeper than in *Quercymegapodius depereti*. Coracoid with a concave scapular facet; below this facet, internal and external sides of the shaft almost parallel. Carpometacarpus with metacarpale majus slender and metacarpale minus very thin; articular facet for digitus minor almost at the same level as facet for digitus major. Smallest species in the genus.

HORIZON AND LOCALITY. Upper Eocene, Phosphorites du Quercy, France.

MEASUREMENTS. See Table 2.

MATERIAL. New excavations: USTL Montpellier:

Lavergne, Upper Eocene: right coracoid, cranial end, LAV 1459.

La Bouffie, Upper Eocene: left coracoid, cranial end, BFI 1849; 2 right humeri, distal end, BFI 1850, 1851.

Rosières 1 and **2,** Upper Eocene: holotype; right tibiotarsus, distal end, ROS 2, 278.

Early Collections without Provenance. MNHN Paris: Right

humerus, proximal end, QU 17030; MNH Basel: Almost complete right carpometacarpus, Q.W. 1574.

DESCRIPTION AND COMPARISONS. This second species of *Quercymegapodius* is represented by only a few remains whose size is smaller than in the type species. Most of the osteological characters agree with those of *Q. depereti.* The only difference is that the pneumatic fossa of the humerus, which is very shallow in *Q. depereti,* is deeper in *Q. brodkorbi.*

ETYMOLOGY. This species is dedicated to Professor Pierce Brodkorb in honor of his eightieth birthday.

Family Phasianidae (Vigors 1825)

Subfamily Phasianinae (Vigors 1825)

Palaeortyx Milne-Edwards 1869

1869	pars	*Palaeortyx* Milne-Edwards, vol. 2, p. 217.
1891	pars	*Palaeortyx* Milne-Edwards: Lydekker, p. 136.
1892	pars	*Palaeortyx* Milne-Edwards: Milne-Edwards, p. 71.
1892	pars	*Rallus sensu* Milne-Edwards: Milne-Edwards, p. 73.
1908	pars	*Palaeortyx* Milne-Edwards: Gaillard, p. 97.
1908	pars	*Rallus* Brisson: Gaillard, p. 109.
1933	pars	*Palaeortyx* Milne-Edwards: Lambrecht, p. 449.
1933	pars	*Quercyrallus* Lambrecht, p. 461.
1964	pars	*Ludiortyx* Brodkorb, p. 298.
1966		*Palaeortyx* Milne-Edwards: Ballmann, p. 47.
1967		*Palaeortyx* Milne-Edwards: Brodkorb, p. 112.
1967	pars	*Quercyrallus* Lambrecht: Brodkorb, p. 118.
1969a		*Palaeortyx* Milne-Edwards: Ballmann, p. 177.
1969b		*Palaeortyx* Milne-Edwards: Ballmann, p. 30.
1973b	pars	*Quercyrallus* Lambrecht: Cracraft, p. 20.
1977	pars	*Quercyrallus* Lambrecht: Olson, p. 344.

DESCRIPTION AND BACKGROUND. The genus *Palaeortyx* was created by Milne-Edwards (1867–1871) and a very complete diagnosis of this genus has been given by Ballmann (1966, 1969a, 1969b). Three species of *Palaeortyx* (*P. brevipes, P. gallica,* and *P. intermedia*), all different in size, occur in the Phosphorites du Quercy. The smallest species, designated *P. ocyptera* by Milne-Edwards, does not differ either morphologically or dimensionally from *P. brevipes* Milne-Edwards, from the Agenian of Saint-Gérand-le-Puy. I therefore place *P. ocyptera* in synonymy with *P. brevipes.* The other two species, not previously known from Quercy, correspond in size to *P. gallica* Milne-Edwards, from the Agenian of Saint-Gérand-le-Puy, and to *P. intermedia* Ballmann 1966, from the Lower Orleanian of Wintershof-West. The measurements of these three species are given in Table 3.

I put into the order Galliformes the femur QU 15568 (MNHN Paris), holotype of the species *Quercyrallus dasypus* Milne-Edwards, 1892 (Figs. 10o, 11b). Phasianid femora look very similar to those of the family Rallidae but differ from them because they are more curved. In the family Rallidae, the femur is curved in both the transverse plane, i.e., both proximal and distal ends are curved mediad, and the sagittal plane, i.e., the shaft of the bone is curved with a posteriorly directed concavity. These two curvatures also exist in the family Phasianidae, but the curvature in the sagittal plane is more pronounced than in the family Rallidae. In the phasianids, the neck of the femur is more marked and the head protrudes more proximad, but these features cannot be seen in the fossil because the head is incompletely preserved.

At the distal end, on the anterior face, the two condyles continue to about the same level in the rallids, whereas in the phasianids the internal condyle ends in a projection but does not extend proximad as much as the external condyle. In distal view, the external and fibular condyles form a large protuberance and are not conspicuously separated in the phasianids, whereas the fibular groove is much more pronounced in the rallids.

The characteristics of the phasianids can be seen on the holotype femur of *Quercyrallus dasypus* and, as its size corresponds to that of *Palaeortyx gallica,* I attribute it to, and place it in synonymy with, this species.

Palaeortyx brevipes Milne-Edwards 1869

Figures 5l, m, 10e, f, l, m, p, 11c, h, i, l–p

1869		*Palaeortyx brevipes* Milne-Edwards, vol. 2, p. 235, pl. 130, figs. 1–21.
1891	pars	*Palaeortyx brevipes* Milne-Edwards: Lydekker, p. 138 (humerus only).
1891	non	*Palaeortyx cayluxensis* Lydekker, p. 138 (see Remarks).
1892		*Palaeortyx ocyptera* Milne-Edwards, p. 71.
1908		*Palaeortyx ocyptera* Milne-Edwards: Gaillard, p. 98, fig. 27, and pl. V, figs. 13–16.
1908	pars	*Palaeortyx Cayluxensis* Lydekker: Gaillard, humerus from Berlin, p. 100, fig. 28, and pl. VI, figs. 1–4, and tarsometatarsus from Mouillac, p. 103, fig. 29.
1933	non	*Palaeortyx cayluxensis* Lydekker: Lambrecht, p. 450.
1933		*Palaeortyx ocyptera* Milne-Edwards: Lambrecht, p. 451.
1933		*Palaeortyx brevipes* Milne-Edwards: Lambrecht, p. 451.
1939		*Palaeortyx* aff. *Cayluxensis* Lydekker: Gaillard, p. 21, fig. 9.
1964	non	*Ludiortyx cayluxensis* (Lydekker): Brodkorb, p. 299.
1964		*Taoperdix brevipes* (Milne-Edwards): Brodkorb, p. 301.
1967		*Palaeortyx brevipes* Milne-Edwards: Brodkorb, p. 112.

REMARKS. I have examined the syntypes of the species *Palaeortyx cayluxensis* Lydekker 1891. These syntypes are two right ulnae, British Museum (Natural History) nos. 137a and 137b, from Caylux (Tarn-et-Garonne, France), purchased in 1884. These two ulnae are not galliforms but, rather, of the family Archaeotrogonidae. According to their size, they correspond to the species *Archaeotrogon zitteli* Gaillard 1908.

MATERIAL. New excavations: USTL Montpellier:

Belgarric 1, Lower Oligocene: left humerus, distal end, BEL 1057.

Pech du Fraysse, Upper Oligocene: radius, distal end, PFY 11282; right tibiotarsus, proximal end, PFY 11281.

Pech Desse, Upper Oligocene: 4 right coracoids, cranial ends, PDS 1266, 1267, 2101, 2102; right coracoid, diaphysis, PDS 1239; left coracoid, cranial end, PDS 2103; complete right humerus, PDS 1298; right humerus, proximal end and diaphysis, PDS 1286; right humerus, distal end, PDS 1300; complete left humerus, PDS 1299; left humerus, distal end, PDS 1265; 2 left ulnae, proximal ends, PDS 1220, 1255; radius, distal end, PDS

Table 3. Dimensions (mm) of the long bones of *Palaeortyx brevipes, P. gallica,* and *P. intermedia* from the Phosphorites du Quercy.

	Palaeortyx brevipes				*Palaeortyx gallica*			
	Mean	**Range**	**s**	**n**	**Mean**	**Range**	**s**	**n**
Coracoid								
Internal length	23.6	—	—	1	25.50	25.2–25.8	0.42	2
Width of cranial end (Fig. 4)	4.05	3.7–4.5	0.28	6	4.57	4.5–4.6	0.06	3
Width of midshaft	2.26	1.8–2.5	0.21	9	2.60	2.5–2.7	0.10	3
Depth of midshaft	1.83	1.6–2.2	0.24	9	2.17	2.0–2.3	0.15	3
Length of sternal facet	6.05	5.8–6.3	0.35	2	—	—	—	—
Humerus								
Total length	34.56	32.6–36.5	1.33	10	40.97	38.8–43.2	2.20	3
Proximal width	8.69	7.9–9.4	0.48	11	11.13	10.4–11.8	0.70	3
Proximal depth	4.11	3.7–4.5	0.22	12	5.16	4.8–5.4	0.26	5
Distal width	6.59	5.8–7.3	0.34	22	7.98	7.5–8.5	0.46	4
Distal depth	3.55	3.1–4.0	0.23	21	4.33	3.9–4.7	0.40	3
Width of midshaft	3.02	2.7–3.4	0.21	22	3.76	3.4–4.0	0.33	5
Depth of midshaft	2.47	2.2–2.7	0.18	22	3.04	2.8–3.3	0.23	5
Ulna								
Total length	—	—	—	—	42.1	—	—	1
Proximal width	4.27	4.1–4.5	0.21	3	4.8	—	—	1
Proximal depth	6.05	6.0–6.1	0.07	2	7.3	—	—	1
Depth of external condyle	—	—	—	—	4.9	—	—	1
Width of midshaft	1.95	1.9–2.0	0.07	2	2.5	—	—	1
Depth of midshaft	2.40	2.3–2.5	0.14	2	3.2	—	—	1
Carpometacarpus								
Total length	19.20	19.0–19.4	0.28	2	20.6	—	—	1
Proximal depth	5.25	5.2–5.3	0.07	2	5.85	5.7–6.0	0.21	2
Width of carpal trochlea	2.67	2.6–2.7	0.06	3	3.05	3.0–3.1	0.07	2
Width of metacarpale majus	1.90	1.8–2.0	0.12	4	2.03	2.0–2.1	0.06	3
Width of metacarpale minus	1.3	—	—	1	1.2	—	—	1
Distal depth	3.50	3.4–3.6	0.10	3	4.0	—	—	1
Distal width	1.97	1.9–2.1	0.12	3	2.3	—	—	1
Femur								
Total length	35.55	34.9–36.2	0.92	2	41.4	—	—	1
Proximal width	6.80	6.3–7.3	0.71	2	—	—	—	—
Proximal depth	4.10	4.0–4.2	0.14	2	—	—	—	—
Distal width	6.49	5.8–7.0	0.32	11	6.8	—	—	1
Distal depth	5.38	4.7–5.8	0.33	12	5.7	—	—	1
Width of midshaft	2.84	2.6–3.3	0.20	12	3.3	—	—	1
Depth of midshaft	2.70	2.3–3.2	0.22	12	2.8	—	—	1
Tibiotarsus								
Total length	56.8	—	—	1	59.7	—	—	1
Proximal width	5.68	5.5–5.8	0.15	4	6.80	6.4–7.2	0.57	2
Proximal depth	7.00	6.9–7.2	0.17	3	8.70	7.7–9.7	1.41	2
Distal width	5.10	4.5–5.4	0.37	6	5.70	5.3–6.1	0.57	2
Distal depth	5.23	4.5–5.7	0.50	6	5.95	5.6–6.3	0.49	2
Width of midshaft	2.80	2.4–3.1	0.36	3	2.95	2.9–3.0	0.07	2
Depth of midshaft	2.53	2.2–2.8	0.31	3	2.90	2.9–2.9	0	2
Tarsometatarsus								
Total length	28.04	26.6–29.0	0.88	7	30.55	30.4–30.7	0.21	2
Proximal width	5.27	4.9–5.5	0.21	9	5.80	5.7–5.9	0.10	3
Proximal depth	4.83	4.5–5.2	0.29	4	5.30	5.2–5.4	0.14	2
Distal width	5.92	5.3–6.1	0.31	6	6.4	—	—	1
Distal depth	3.73	3.6–4.0	0.23	3	c. 4.3	—	—	1
Width of midshaft	2.67	2.3–3.0	0.22	9	2.95	2.9–3.0	0.07	2
Depth of midshaft	2.03	1.8–2.3	0.17	9	2.30	2.3–2.3	0	2

Table 3. Continued.

Palaeortyx intermedia			
Mean	**Range**	**s**	**n**
31.70	29.5–34.8	2.76	3
5.68	4.9–6.7	0.78	4
3.37	3.1–3.8	0.38	3
2.77	2.4–3.2	0.40	3
6.45	6.4–6.5	0.07	2
53.4	—	—	1
12.50	12.2–12.8	0.42	2
5.95	5.5–6.4	0.64	2
10.10	9.6–10.4	0.44	3
5.43	4.9–5.8	0.47	3
4.63	4.2–5.0	0.40	3
3.80	3.4–4.1	0.36	3
—	—	—	—
—	—	—	—
—	—	—	—
—	—	—	—
—	—	—	—
—	—	—	—
23.0	—	—	1
7.30	7.2–7.4	0.14	2
3.55	3.5–3.6	0.07	2
2.63	2.4–2.8	0.21	3
—	—	—	—
4.5	—	—	1
2.6	—	—	1
—	—	—	—
9.2	—	—	1
5.3	—	—	1
—	—	—	—
—	—	—	—
3.6	—	—	1
3.2	—	—	1
—	—	—	—
—	—	—	—
—	—	—	—
—	—	—	—
—	—	—	—
—	—	—	—
—	—	—	—
—	—	—	—
—	—	—	—
—	—	—	—
—	—	—	—
—	—	—	—

1283; right femur, proximal end, PDS 1217; 2 right femora, distal ends, PDS 1225, 2105; left femur, distal end, PDS 2104; right tibiotarsus, distal end, PDS 1262; left tibiotarsus, proximal end, PDS 1229; left tibiotarsus, distal end, PDS 2106; right tarsometatarsus, distal end, juvenile, PDS 1263; right tarsometatarsus, fragment of distal end, PDS 2107.

MNHN Paris:

Pech du Fraysse, Upper Oligocene: right coracoid, cranial end, PFR 11104; left coracoid, cranial end, PFR 11283; right humerus, proximal end, PFR 11155; 2 right humeri, distal ends, PFR 5115, 11285; right humerus, diaphysis, PFR 11183; left humerus, proximal end, PFR 11041; 3 left humeri, distal ends, PFR 7219, 11030, 11284; right scapula, proximal end, PFR 11286; right ulna, proximal end, PFR 11094; right carpometacarpus, distal end, PFR 596; left carpometacarpus, proximal end, PFR 11119; 3 right femora, distal end, PFR 11037, 11044, 11087; left femur, distal end, PFR 11027; right tibiotarsus, proximal end, PFR 11154; right tibiotarsus, distal end, PFR 11010; 2 left tibiotarsi, distal ends, PFR 5117, 11122; almost complete right tarsometatarsus, PFR 11217; complete left tarsometatarsus, PFR 11078; left tarsometatarsus, distal end, PFR 11287.

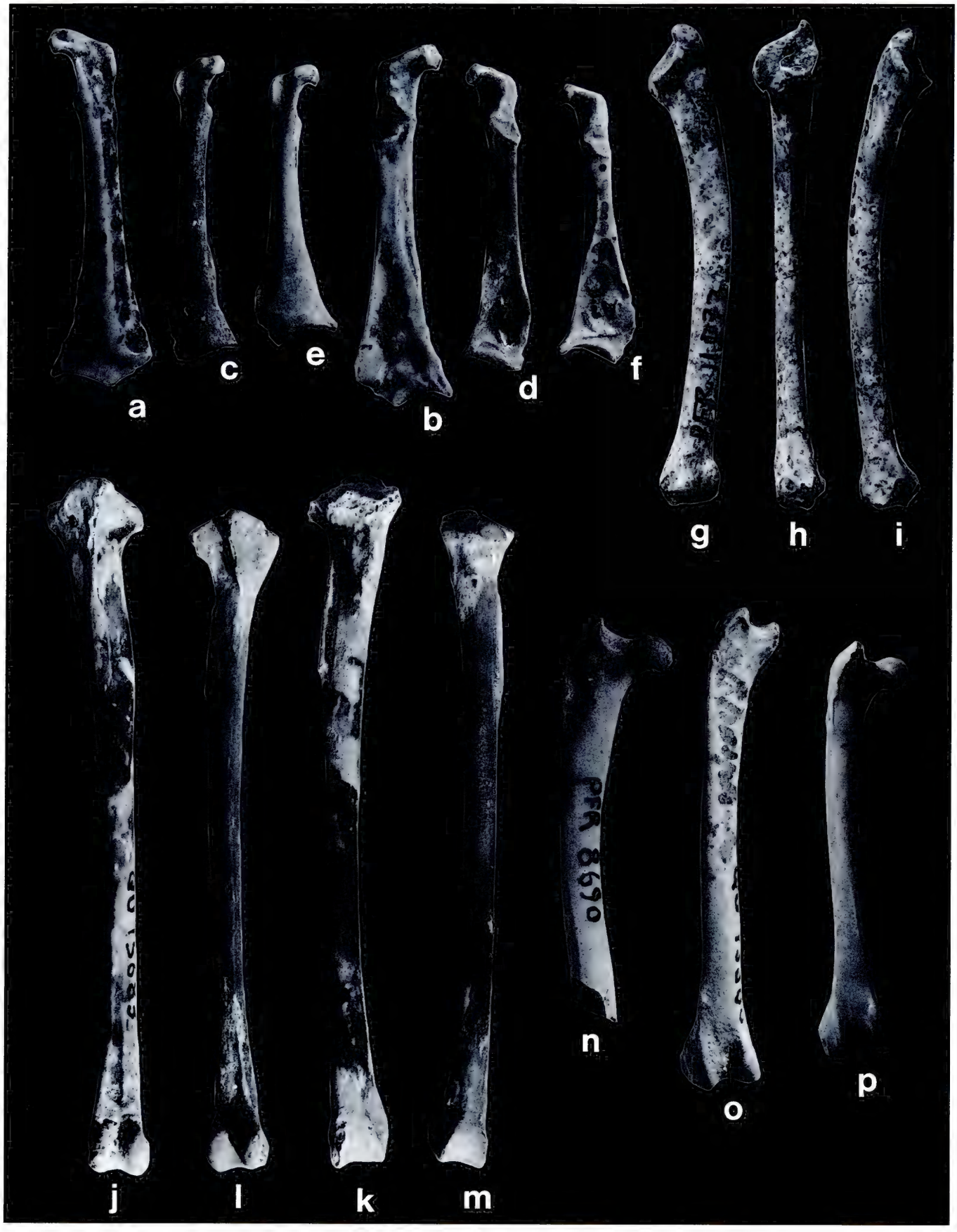
Early Collections without Provenance. MNHN Paris: Almost complete right coracoid, QU 15593 (formerly no. 3093) (was a part of the type material of *Palaeortyx ocyptera*); complete right humerus, QU 15586; 2 right humeri, distal ends, QU 15575, 17028; 4 complete left humeri, QU 15592 (formerly no. 3092) (holotype of *P. ocyptera*), 15587, 15591, 15595; almost complete left humerus, QU 15597; left humerus, proximal end, juvenile, QU 15584; 3 left humeri, distal ends, QU 15590, 15594, 15875; almost complete right carpometacarpus, QU 17031; almost complete left carpometacarpus, QU 15638; 2 almost complete right femora, QU 17002, 17027; 3 left femora, distal ends, QU 15686, 15687, 16934; complete right tibiotarsus, QU 16964; 3 almost complete right tarsometatarsi, QU 16967, 16970, 16971; right tarsometatarsus, proximal end, QU 15577; almost complete left tarsometatarsus, QU 16969. MGHN Lyon: Cast of a complete left humerus from the Berlin Museum, PQ 1080. University of Marseille: Complete right humerus, illustrated in Gaillard (1939:21, fig. 9). MNH Basel: Incomplete right coracoid, Q.D. 574; complete right humerus, Q.D. 404; right femur, distal end, Q.W. 507; left femur, distal end, Q.O. 597; incomplete right tarsometatarsus, Q.F. 598; incomplete left tarsometatarsus, number not legible.

MEASUREMENTS. See Table 3.

Palaeortyx gallica Milne-Edwards 1869

Figures 5j, k, 10c, d, g–k, o, 11b, f, g, j, k, q

1869	pars	*Palaeortyx gallica* Milne-Edwards, vol. 2, p. 230, pls. 128, 129 (see Remarks).
1891	non	(?)*Palaeortyx gallica* Milne-Edwards: Lydekker, p. 137 (see Remarks).
1892		*Rallus dasypus* Milne-Edwards, p. 73.
1908		*Rallus dasypus* Milne-Edwards: Gaillard, p. 112.
1933		*Palaeortyx gallica* Milne-Edwards: Lambrecht p. 452.
1933		*Quercyrallus dasypus* (Milne-Edwards): Lambrecht, p. 461.
1964		*Taoperdix gallica* (Milne-Edwards): Brodkorb, p. 301.
1967		*Palaeortyx gallica* Milne-Edwards: Brodkorb, p. 112.


a
c
e
b
d
f
g
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k
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n
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p

1967 *Quercyrallus dasypus* (Milne-Edwards): Brodkorb, p. 118.
1973b *Quercyrallus dasypus* (Milne-Edwards): Cracraft, p. 24, fig. 10d, e.
1977 *Quercyrallus dasypus* (Milne-Edwards): Olson, p. 344.

REMARKS. According to Ballmann (1966, 1969b), the ulna illustrated by Milne-Edwards (1869:pl. 129, figs. 23, 24) as belonging to *Palaeortyx gallica* actually belongs to a psittaciform, which is probably *Archaeopsittacus verreauxi* (Milne-Edwards 1870). The coracoid illustrated by Lydekker (1891:138, fig. 33) under the name of (?)*Palaeortyx gallica* corresponds in size to the largest of the three species of the genus *Palaeortyx* found in Quercy, *P. intermedia*.

MATERIAL. New excavations: USTL Montpellier:

Pech Desse, Upper Oligocene: right coracoid, cranial end, PDS 2108; almost complete left coracoid, juvenile, PDS 1288; almost complete left humerus, PDS 2109; right tarsometatarsus, proximal end, PDS 1261.

MNHN Paris:

Pech du Fraysse, Upper Oligocene: right coracoid, cranial end, PFR 11221; left scapula, proximal end, PFR 11219; 2 right humeri, proximal ends, PFR 11023, 11035; right humerus, distal end, PFR 11173; complete right ulna, PFR 11077; almost complete right carpometacarpus, PFR 11118; left carpometacarpus, distal end, PFR 11199; left tibiotarsus, proximal end, PFR 11181; 2 left tibiotarsi, distal part, PFR 11049, 11184 (juv.); almost complete right tarsometatarsus, PFR 11017.

Early Collections without Provenance. MNHN Paris: Almost complete right coracoid, QU 15912; almost complete left humerus, QU 15532; almost complete left carpometacarpus, QU 15889; almost complete right femur, QU 15568 [formerly no. 3068, holotype of the species *Quercyrallus dasypus* (Milne-Edwards)]; complete left tibiotarsus, QU 15683; complete right tarsometatarsus, QU 16972. MNH Basel: Almost complete left coracoid, Q.H. 111.

MEASUREMENTS. See Table 3. The comparisons between the measurements given by Milne-Edwards (1869:vol. 2, 237) for the species *Palaeortyx brevipes* and *P. gallica* from Saint-Gérand-le-Puy and those of Quercy specimens are presented in Table 4.

Palaeortyx intermedia Ballmann 1966

Figures 5h, i, 10a, b, n, 11a, d, e

1891 (?)*Palaeortyx gallica* Milne-Edwards: Lydekker, p. 137–38, fig. 33.
1966 *Palaeortyx* ? *intermedia* Ballmann, p. 54, pl. 1, fig. 3.
1967 *Palaeortyx intermedia* Ballmann: Brodkorb, p. 112.
1969b *Palaeortyx* ? *intermedia* Ballmann: Ballmann, p. 33, pl. 1, figs. 1, 2.

MATERIAL. New excavations: USTL Montpellier:

Pech Desse, Upper Oligocene: right tarsometatarsus, distal end, PDS 1240.

MNHN Paris:

Pech du Fraysse, Upper Oligocene: right coracoid, cranial end, PFR 11222; complete left coracoid, PFR 590; right humerus, proximal end, PFR 11020; right humerus, distal end, PFR 11014; incomplete right carpometacarpus, PFR 11048; right femur, proximal end, PFR 8690.

Early Collections without Provenance. MNHN Paris: 2 almost complete left coracoids, QU 16935, 17001; complete left humerus, QU 15582; left humerus, distal end, QU 16962; left carpometacarpus, proximal end, QU 16936. MNH Basel: Almost complete right carpometacarpus, Q.U. 114.

MEASUREMENTS. See Table 3. The comparisons between the measurements given by Ballmann (1966, 1969b) for the species *Palaeortyx intermedia* from Wintershof-West and those of Quercy specimens are given in Table 5.

COMPARISONS WITH OTHER FOSSIL FORMS. In addition to the morphological differences described earlier, the genus *Palaeortyx* differs from *Paraortyx* by the proportions of the main long limb bones. In *Palaeortyx*, the femur and the tarsometatarsus are proportionally shorter and the tibiotarsus much longer than in *Paraortyx*. The genus *Schaubortyx* was established by Brodkorb (1964) for the species *Taoperdix keltica* Eastman 1905, from the Oligocene of Armissan, France, and placed in the family Phasianidae. Unlike what was written by Brodkorb (1964:113) in his diagnosis, the intermetacarpal tuberosity is present in *Palaeortyx* spp. *Schaubortyx keltica* is represented by a complete skeleton, on a slab, in the collection of the Carnegie Museum, Pittsburgh, U.S.A. (Eastman, 1905), and the reverse is in the collection of the MNH Basel (Schaub, 1945). It is not possible to observe in detail all the morphological features of the bones in *S. keltica*, but it differs from *Palaeortyx* spp. by its proportions. Its femur and tarsometatarsus are proportionally longer and its tibiotarsus shorter than in *Palaeortyx* spp. (Fig. 12).

SYSTEMATIC POSITION OF THE GENUS *PALAEORTYX*

Ballmann (1966, 1969b) has carried out a detailed analysis of the systematic affinities of the genus *Palaeortyx*. His conclusions are that *Palaeortyx* is not related to the subfamily Odontophorinae but is more closely related to the group of tree-partridges, in the subfamily Phasianinae, and particularly to the genus *Arborophila*. This group is widespread in the tropical and subtropical regions of Southeast Asia and Africa, including Madagascar.

FORM INCORRECTLY ASCRIBED TO THE SUBFAMILY NUMIDINAE REICHENBACH 1850

Mlíkovský (1989) described a fossil galliform from the Phosphorites du Quercy, which had been kept in the collection of

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Figure 10. *Palaeortyx intermedia:* left coracoid, MNHN Paris, PFR 590, in ventral (**a**) and dorsal (**b**) views, ×2. *Palaeortyx gallica:* right coracoid, MNHN Paris, QU 15912, in ventral (**c**) and dorsal (**d**) view, ×2. *Palaeortyx brevipes:* right coracoid, MNHN Paris, QU 15593, in ventral (**e**) and dorsal (**f**) views, ×2. *P. gallica:* right ulna, MNHN Paris, PFR 11077, in internal (**g**), palmar (**h**), and external (**i**) views, ×2; left tibiotarsus, MNHN Paris, QU 15683, in anterior (**j**) and posterior (**k**) views, ×2. *P. brevipes,* left tibiotarsus, MNHN Paris, QU 16964, in anterior (**l**) and posterior (**m**) views, ×2. *P. intermedia:* right femur, proximal end, MNHN Paris, PFR 8690, in anterior (**n**) view, ×2. *P. gallica:* right femur, MNHN Paris, QU 15568, formerly holotype of the species *Quercyrallus dasypus,* in anterior (**o**) view, ×2. *P. brevipes:* right femur, MNHN Paris, QU 17027, in anterior (**p**) view, ×2.

a
b
c
d
f
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q

Table 4. Comparisons between the dimensions (mm) of Quercy forms of *Palaeortyx brevipes* and *Palaeortyx gallica* and those given by Milne-Edwards (1869 (2):327) for the Saint-Gérand-le-Puy forms. (a), measurements concerning only the QU 15593 specimen.

	Palaeortyx brevipes		*Palaeortyx gallica*	
	Quercy mean (n)	St. Gérand after Milne-Edwards	Quercy mean (n)	St. Gérand after Milne-Edwards
Humerus				
Total length	34.6 (10)	35.7	41.0 (3)	42.5
Proximal width	8.7 (11)	8.5	11.1 (3)	10.1
Distal width	6.6 (22)	6.9	8.0 (4)	7.9
Width of midshaft	3.0 (22)	2.9	3.8 (5)	3.9
Depth of midshaft	2.5 (22)	2.5	3.0 (5)	3.0
Coracoid				
External length	25.0 (a)	25.0	—	—
Length sternal facet	6.05 (2)	5.5	—	—
Width below the scapular facet	2.2 (a)	2.0	—	—
Width at the level of the glenoid facet	3.0 (a)	3.0	—	—
Femur				
Total length	35.6 (2)	32.9	41.4 (1)	42.0
Proximal width	6.8 (2)	6.0	—	7.0
Distal width	6.5 (11)	5.0	6.8 (1)	6.8
Width of midshaft	2.8 (12)	2.0	3.3 (1)	3.0
Depth of midshaft	2.7 (12)	2.0	2.8 (1)	3.0
Tibiotarsus				
Total length	—	—	59.7 (1)	58.7
Proximal width	—	—	6.8 (1)	7.0
Proximal depth	—	—	8.7 (2)	8.0
Distal width	—	—	5.7 (2)	5.0
Width of midshaft	—	—	3.0 (2)	2.8
Depth of midshaft	—	—	2.9 (2)	2.5
Tarsometatarsus				
Total length	28.0 (7)	27.0	30.6 (2)	34.8
Proximal width	5.3 (9)	4.9	5.8 (3)	5.8
Proximal depth	—	—	5.3 (2)	5.4
Distal width	5.9 (6)	4.9	6.4 (1)	6.0
Width of midshaft	2.7 (9)	2.2	3.0 (2)	2.9
Depth of midshaft	2.0 (9)	2.0	2.3 (2)	2.0

the Naturhistorisches Museum Wien, Austria, as *Telecrex peregrinus* new species, family Phasianidae, subfamily Numidinae. The holotype is an almost complete left femur, n° 1988/28/1; the material also includes another almost complete left femur, n° 1988/28/2. The illustration of the holotype shows that it is similar in every respect to the femora attributed to *Elaphrocnemus phasianus* Milne-Edwards 1892, order Gruiformes, family Cariamidae, subfamily Idiornithinae (Mourer-Chauviré, 1983: pl. 1, figs. 14, 15). This species is very abundant in the Quercy deposits and the femora are represented by 25 complete or almost complete specimens and 9 proximal or distal parts.

This femur can be distinguished from that of galliforms by the following characteristics: Head proportionally more projecting on the internal side; on the anterior face, at the proximal end, intermuscular line running parallel to the trochanteric ridge, at some distance from it; distinct ridge along the anterior edge of the proximal articular surface that connects the head to the trochanter much more pronounced; at the distal end, rotular

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Figure 11. *Palaeortyx intermedia:* right femur, proximal end, MNHN Paris, PFR 8690, in posterior (**a**) view, ×2. *Palaeortyx gallica:* right femur, MNHN Paris, QU 15568, formerly holotype of the species *Quercyrallus dasypus,* in posterior (**b**) view, ×2. *Palaeortyx brevipes:* right femur, MNHN Paris, QU 17027, in posterior (**c**) view, ×2. *P. intermedia:* right carpometacarpus, MNH Basel, QU 114, in internal (**d**) and external (**e**) views, ×2. *P. gallica:* right carpometacarpus, MNHN Paris, PFR 11118, in internal (**f**) and external (**g**) views, ×2. *P. brevipes:* left carpometacarpus, MNHN Paris, QU 15638, in internal (**h**) and external (**i**) views, ×2. *P. gallica:* right tarsometatarsus, MNHN Paris, QU 16972, in anterior (**j**) and posterior (**k**) views, ×2. *P. brevipes:* right tarsometatarsus, MNHN Paris, QU 16971, in anterior (**l**) and posterior (**m**) views, ×2; radius, distal end, USTL, PFY 11282, in anconal (**n**) and palmar (**o**) views, ×2; right scapula, proximal end, MNHN Paris, PFR 11286, in dorsal (**p**) view, ×2. *P. gallica:* left scapula, proximal end, MNHN Paris, PFR 11219, in dorsal (**q**) view, ×2. Galliformes *incertae sedis:* right tarsometatarsus, MNHN Paris, QU 15536, in anterior (**r**) and posterior (**s**) views, ×2.

Table 5. Comparison between the dimensions (mm) given by Ballmann (1969b) for the Wintershof-West form of *Palaeortyx intermedia* and those of Quercy forms. The specimen A.137 is preserved in the collections of the British Museum (Natural History). (a), from the glenoid facet to the margo intermuscularis.

	Palaeortyx intermedia Wintershof-West holotype	*Palaeortyx intermedia* Quercy			
		PFR 590	QU 16935	QU 17001	A. 137
Coracoid					
External length	35	c. 32	32.0	36.5	c. 35
Length of sternal facet	7	c. 6.5	c. 6.5	—	—
Width below the scapular facet	3	3.0	2.8	3.5	—
Width at the level of the collum acrocoracoidei (a)	4	3.8	3.6	4.8	—

groove proportionally much narrower and more oblique; popliteal fossa deeper. Moreover, in external view the femur of the galliforms, as well as that of *Telecrex grangeri* Wetmore 1934, is much more posteriorly incurved. The dimensions of both specimens of *Telecrex peregrinus* are within the range of variation of *Elaphrocnemus phasianus*.

In conclusion, the presence of the subfamily Numidinae in the Eocene of Phosphorites du Quercy is so far unproved and must be deleted from the paleornithological literature.

Galliformes *incertae sedis*

Figure 11r, s

I have put into Galliformes *incertae sedis* a complete tarsometatarsus, QU 15536, from the MNHN Paris, and some distal ends of tarsometatarsi from the old collections. The complete tarsometatarsus differs from that of *Paraortyx* and *Palaeortyx* in having, below the proximal articular part, a deep anterior metatarsal groove, the vault of which makes a kind of ogive, and in the bottom of which the two proximal foramina are open.

The hypotarsus has three ridges: the internal one projects farthest posteriad, an external ridge that widens at its distal end, and a supplementary one on the external side. The space between the internal and external ridges is occupied by a groove that is incompletely roofed by a bone. The groove for the m. flexor perforatus digiti 2 and m. flexor perforans and perforatus digiti 2 (groove 4 of Ballmann, 1969b), and the canal for the tendon of the m. flexor digitorum longus, are thus incompletely separated, whereas they are completely separated in *Paraortyx* and *Palaeortyx*.

This large-sized tarsometatarsus (length, 48 mm) could possibly be attributed to the genus *Pirortyx*, of which only the humerus is known, but it is not possible to confirm this because these two elements have not been found together in the same locality.

STRATIGRAPHIC POSITION

The occurrence of the taxa at the different localities is indicated in Fig. 13. The stratigraphic order of the localities is founded on the studies of L. de Bonis, J.Y. Crochet, J.L. Hartenberger, J.C. Rage, B. Sigé, J. Sudre, and M. Vianey-Liaud (de Bonis et al., 1973; Crochet et al., 1975, 1981). The denomination of the mammalian standard-levels is the one adopted during the Mainz Symposium (Schmidt-Kittler, 1987). It appears that during the Eocene the order Galliformes was represented in Quercy by species of the families Gallinuloididae, Paraortygidae, and Quercymegapodiidae.

The Phasianidae appear in the Quercy deposits at the end of the Lower Oligocene, in the locality of Belgarric. They are also known in the Oligocene of Armissan, France, in the form of *Schaubortyx keltica* (Eastman). According to the degree of evolution of the *Suevosciurus* Dehm 1937 found at this locality (Schmidt-Kittler, 1971), Armissan can be dated from the end of the Lower Oligocene. The age of this site is in perfect agreement with that of Belgarric, i.e., mammal standard-level of Garouillas, MP 25 (Schmidt-Kittler, 1987), or old standard-level of Antoingt (Fahlbusch, 1976).

It is therefore likely that the family Phasianidae appeared in France at the end of the Early Oligocene and superceded all other families of the order Galliformes. However, this replacement was carried out very gradually, for the Paraortygidae persisted into the Late Oligocene (with *Pirortyx major*), the Gallinuloididae into the Early Miocene [with *Taoperdix miocaena* (Ballmann, 1969b)], and the Quercymegapodiidae also into the Early Miocene (with the as-yet-undescribed remains from Saint-Gérand-le-Puy).

PALEOBIOGEOGRAPHICAL IMPLICATIONS

The occurrence in the Quercy deposits of the primitive family Quercymegapodiidae, related to Recent mound builders, although not directly ancestral to them, shows that primitive galliforms were probably widespread during the Paleogene and that their present distribution is a relictual one. As Olson (1980) emphasized, the distribution of the family Megapodiidae is complementary to that of the family Phasianidae and the megapodes may have been pushed back into the areas where they now live by the Phasianidae when the latter diversified and progressively occupied all the Eurasiatic continent. There are also several other groups in the Quercy whose distribution, Recent or fossil, is, or was, very different, e.g., the Vulturidae (=Cathartidae *auct.*) (Cracraft and Rich, 1972), the Sagittariidae (Mourer-Chauviré and Cheneval, 1983), the Cariamidae, Phorusrhacidae, Coliidae, Todidae, Podargidae, Nyctibiidae, Psittacidae, etc. (Mourer-Chauviré, 1982, 1983, 1985, 1988, 1989). This suggests that, for all of these groups, their distribution, Recent or fossil, does not correspond to their place of origin. Rather, the extant forms are probably relicts of very widespread groups that diversified in the distant past.

PHYLOGENETIC IMPLICATIONS

Figure 14 represents an attempt to place the fossil galliforms from Quercy in the phylogenetic sequence of their Recent relatives. The family Gallinuloididae is not included in this diagram because the shape of the scapular facet on the coracoid is not known in the fossils attributed to this family, and it is also not known if the humeral head presents an extension that meets the medial bar of the internal tuberosity. The branching order and

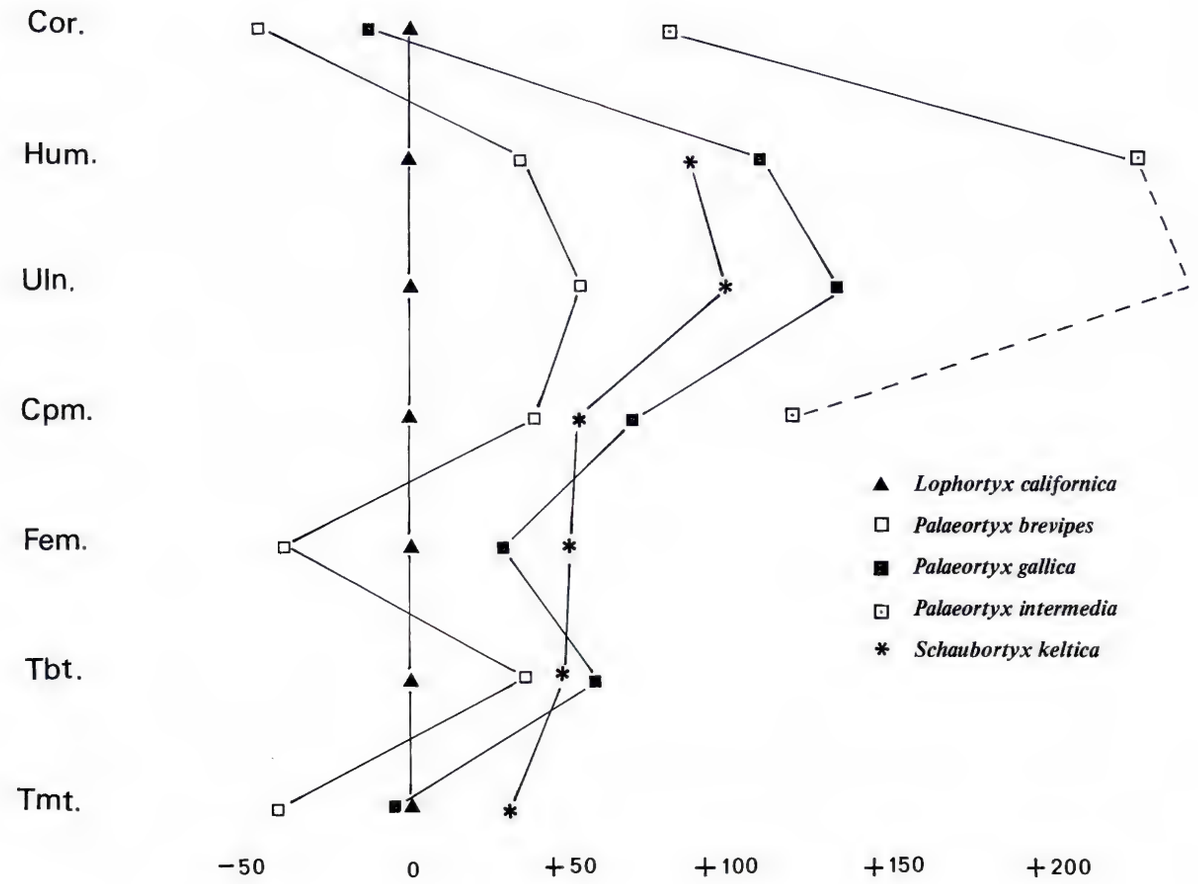


Figure 12. Simpson's (1941) ratio-diagram of the log differences of the main long bones in the different species of *Palaeortyx* and in *Schaubortyx* (measurements of Schaub, 1945). The Recent *Lophortyx californica* has been taken as standard. For the length of the ulna in *P. gallica* and *P. brevipes*, I have used specimens from the locality Saint-Gérand-le-Puy.

the relationships of the Recent families of the Galliformes and Anseriformes are founded on the works of Sibley et al. (1988) on DNA-DNA hybridization. The Recent family Phasianidae of Morony et al. (1975) is here split into three different families: Odontophoridae, Numididae, and Phasianidae. The primitive character: Capital groove open into the tricipital fossa (1) is found in Paraortygidae and the Recent Anseriformes, and the derived character: Capital groove closed by an extension of the humeral head (2) is found in Quercymegapodiidae and the Recent Galliformes. The primitive character: Concave scapular facet on the coracoid (3) is found in Paraortygidae, Quercymegapodiidae, and the Recent Anseriformes, and the derived character: Superficial, not concave, scapular facet (4) in this study was found only in the Recent Galliformes.

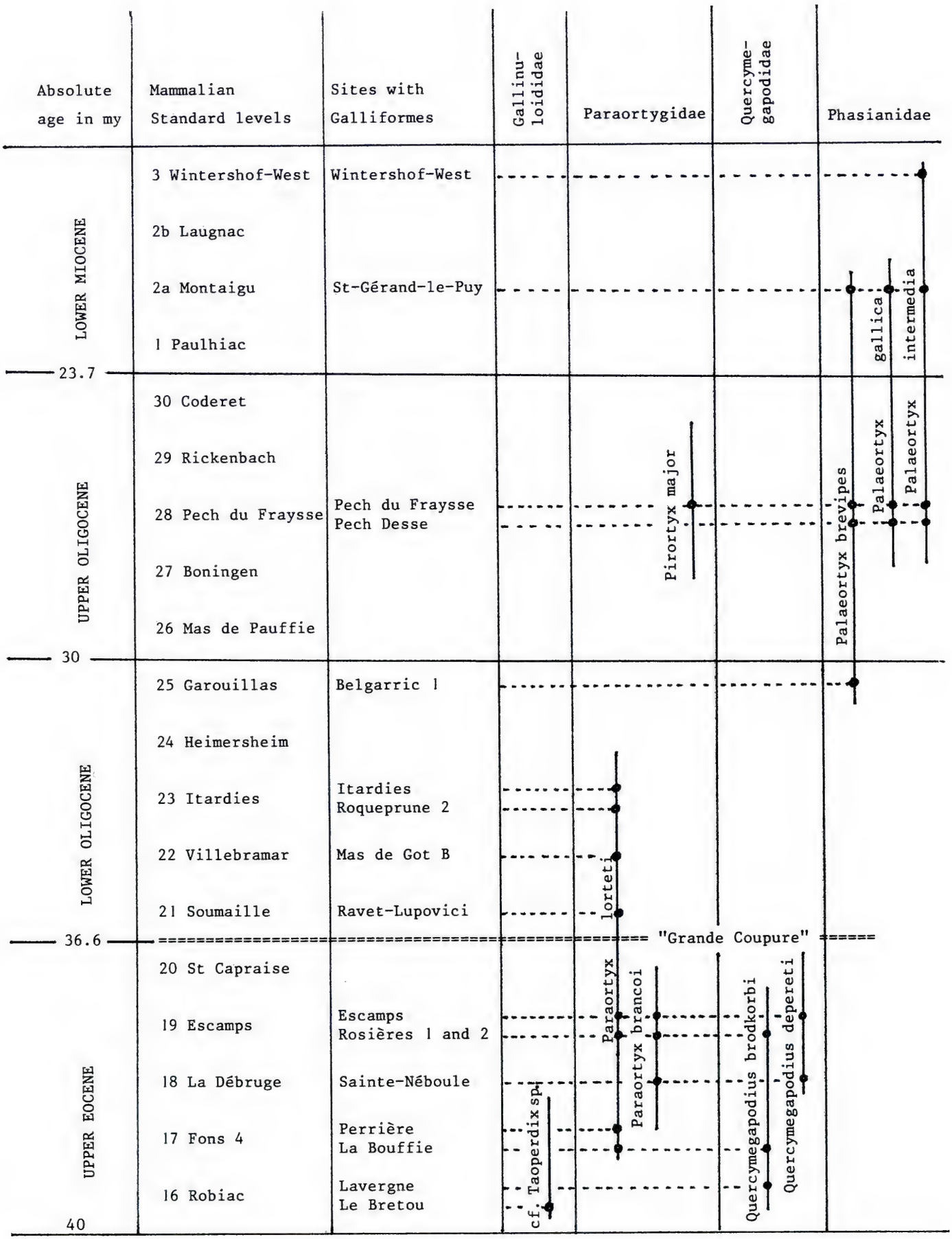
In the Paraortygidae, the different species of the genus *Paraortyx* have a very deep tricipital fossa that extends deeply under the humeral head, which is a derived character. The genus *Pirortyx* does not present this character, but in the Recent subfamily Phasianinae the depth of the tricipital fossa also exhibits a great variability.

The Quercymegapodiidae share with the Recent Megapodiidae the attachment of m. latissimus dorsi on the external side of the shaft of the humerus, whereas in all the other Galliformes, the attachment of this muscle is situated on the internal side of the shaft. This latter character probably represents the primitive condition in birds. If the character "Capital groove open into the tricipital fossa" is not the primitive condition but a reversal to a primitive condition, this would also imply a reversal to a primitive condition in the shape of the scapular articular facet of the coracoid, which seems unlikely.

CONCLUSIONS

The most important results of the study of the Quercy galliforms are the bringing to light of two primitive galliform families in Europe during the Eocene and Oligocene and the dating of the first appearance of the Phasianinae in Europe to the end of the Early Oligocene.

Based on the geographic distribution of the Recent families, Cracraft (1973a:507) suggested a Gondwanaland origin for the Galliformes. The present insufficiency of the fossil record in the continents arising from the breaking up of Gondwanaland does not make it possible to bring arguments in favor of, or against, this hypothesis. The occurrence of the Paraortygidae and Quercymegapodiidae in the Quercy deposits shows that during the Eocene the Galliformes were already diversified and that primitive families of that order were already in existence in Europe. For a better understanding of the relationships between these forms and other previously described fossil galliforms, it should be necessary to revise the different forms attributed to the family Gallinuloididae, with additional preparation of the holotypes, as suggested by Olson (1985).


Absolute age in my
Mammalian Standard levels
Sites with Galliformes
Gallinuloididae
Paraortygidae
Quercymegapodidae
Phasianidae
LOWER MIOCENE
UPPER OLIGOCENE
LOWER OLIGOCENE
UPPER EOCENE
3 Wintershof-West
2b Laugnac
2a Montaigu
1 Paulhiac
23.7
30 Coderet
29 Rickenbach
28 Pech du Fraysse
27 Boningen
26 Mas de Pauffie
30
25 Garouillas
24 Heimersheim
23 Itardies
22 Villebramar
21 Soumaille
36.6
20 St Capraise
19 Escamps
18 La Débruge
17 Fons 4
16 Robiac
40
Wintershof-West
St-Gérand-le-Puy
Pech du Fraysse
Pech Desse
Belgarric 1
Itardies
Roqueprune 2
Mas de Got B
Ravet-Lupovici
"Grande Coupure"
Escamps
Rosières 1 and 2
Sainte-Néboule
Perrière
La Bouffie
Lavergne
Le Bretou
Pirortyx major
lorteti
Paraortyx
Paraortyx brancoi
cf. Taoperdix sp.
Quercymegapodius brodkorbi
Quercymegapodius depereti
Palaeortyx brevipes
Palaeortyx
gallica
Palaeortyx
intermedia

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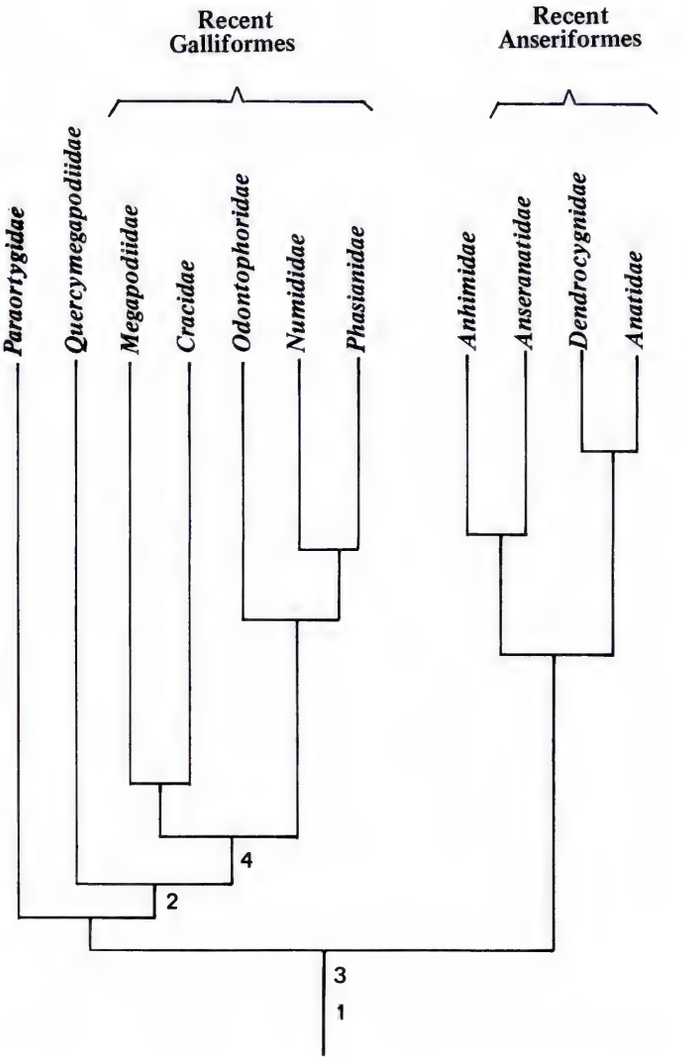

Figure 14. Hypothetical phylogenetic positions of the fossil galliforms from Quercy. The branching order and the relationships of the Recent Galliformes and Anseriformes are founded on the works of Sibley et al. (1988). **1.** Humerus with capital groove open into the tricipital fossa. **2.** Capital groove closed by an extension of the humeral head. **3.** Coracoid with concave scapular facet. **4.** Coracoid with superficial, not concave, scapular facet.

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Figure 13. Temporal distribution of galliforms in the localities of Phosphorites du Quercy.

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THE STATUS OF THE LATE PALEOCENE BIRDS *GASTORNIS* AND *REMIORNIS*

Larry D. Martin

ABSTRACT. A reexamination of the fossil birds described from the Upper Paleocene of France by Lemoine shows that most aspects of his restoration of *Gastornis* are incorrect. *Gastornis* is very similar to, but not congeneric with, *Diatryma*. The species *Gastornis minor* is a *nomen dubium* and should not be confused with *Remiornis heberti*. *Remiornis* is an early, giant, flightless bird whose affinities lie with modern ratites. A new species of gastornithid, *Gastornis russelli*, is described, and a new order, Remiornithiformes, and family, Remiornithidae, are erected for *Remiornis*.

Key words: Paleocene, Aves, *Gastornis, Remiornis, Diatryma,* flightlessness, ratites.

INTRODUCTION

The Museum national d'Histoire Naturelle in Paris contains not only important type material of fossil birds from the last century, but also an extensive new collection of Paleocene birds made by D.E. Russell as a by-product of his Paleocene mammal collecting (Russell, 1964). These collections provide an opportunity to reevaluate the genus *Gastornis* Hébert 1855.

Gastornis may be compared to another giant early Tertiary bird, *Diatryma* Cope 1876. Lemoine (1881) published a restored skeleton of *Gastornis* and Matthew and Granger (1917) illustrated a skeleton of *Diatryma*. Comparisons of the two restorations indicated a considerable morphological distance between the two birds, and, as a result, they have been placed in separate families, the Gastornithidae and Diatrymidae. Some workers have also recognized these two groups at an ordinal level [see Brodkorb (1967) for a review]. Most recent workers have placed them close to the order Gruiformes (Brodkorb, 1967; Feduccia, 1980), although Olson (1985) and Andors (1988) doubt that they have any affinity with cranes.

The type "skeleton" of *Gastornis edwardsii* Lemoine 1878 illustrated by Lemoine (1881:pl. 11) was lost for some time, but with the help of the staff of the Museum national d'Histoire Naturelle, Paris, I was able to relocate it. It had gone unrecognized because it had been dismantled and consisted of isolated fragments that did not come from any single individual. Study of the Lemoine collection showed that most of the supposed differences from *Diatryma* were the result of errors of identification and that the two forms were much more similar than was generally supposed (Martin, 1983).

Lemoine's material was unnumbered and could only be identified by comparison with his figures (Lemoine, 1878, 1881). His figures are drawn life-sized and reversed, but they do show diagnostic details of preservation that permit identification of individual specimens. The following lists include many tentative identifications owing to the fragmentary condition of the specimens and the inclusion of fish and reptile material. All of the material is part of the syntypic series of *Gastornis edwardsii* or *Remiornis herberti* Lemoine 1881, but as these were described as birds I have restricted detailed systematic considerations to the material that is clearly avian. Lemoine's descriptions are published in a two-volume set, but the plates are numbered sequentially so that pls. 1–5 are in volume 1, published in 1878, and pls. 6–11 are in volume 2, published in 1881.

Plate 1 of Lemoine (1878) depicts a femur (CRL 2460) whose indicated length seems to be too long. Plate 3, figs. 1–3, shows a restored tarsometatarsus (CRL 2458) of *Gastornis* that upon examination proves to be lengthened to about double its actual length through the addition of plaster and fragments from a tibia and femur. No actual contacts exist between the trochleae, but they seem to form a set and appear to be from an immature bird. The illustrated vertebra (CRL 2459) also seems to be from *Gastornis*.

Plate 5 of Lemoine (1878) shows a left tibiotarsus (CRL 2457) of *Gastornis edwardsii*. Plate 6, figs. 4, 5 (Lemoine, 1881), depicts a fairly well preserved distal end of a tibiotarsus of *Gastornis*. Plate 6, figs. 6–9, is of phalanges (CRL 2467, CRL 2465, CRL 2466, CRL 2468) that might pertain to *Gastornis*, as does the phalanx shown in pl. 6, fig. 11. Plate 6, figs. 10, 12, may be turtle (CRL 2471) or champsosaur (CRL 2469). Plate 7 (Lemoine, 1881) includes a *Gastornis* ischium (CRL 2462) (fig. 3), caudal vertebrae (CRL 2463) (figs. 4–9), and rib (CRL 2464) (fig. 10). Plate 7, fig. 14 (CRL 2472), may be a distal end of a rib, whereas the putative pubis (CRL 2467) (pl. 7, figs. 1, 2) is probably a fish premaxilla.

The bones illustrated in pl. 8 of Lemoine (1881) do not seem to be avian. The specimens corresponding to figs. 9–11 (champsosaur fibula?), 16–20, and 23 could not be located. The specimens corresponding to the following figures of Lemoine (1881: pl. 8) were found: figs. 1, 3 (champsosaur clavicle); figs. 2, 4, 5 (upper portion, turtle pelvis; lower portion not relocated); figs. 6–8 (turtle humerus, CRL 2521); figs. 12–15 (CRL 2470, turtle

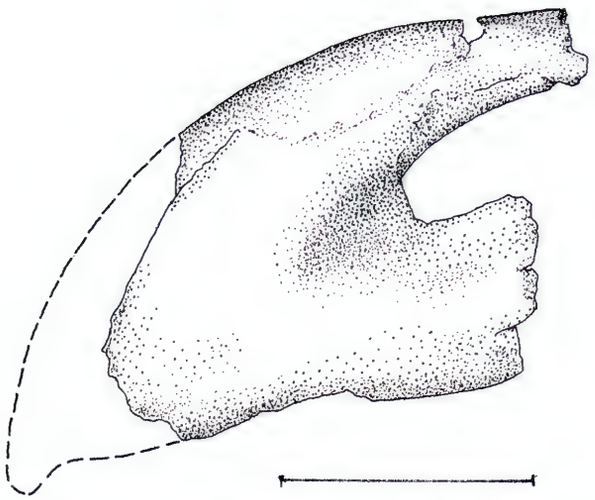

Figure 1. Lateral view of bill, R 2583, tentatively referred to *Gastornis russelli* n. sp. Scale bar = 5 cm.

fibula?); figs. 21–23 (CRL 2473; unidentified, but not avian); figs. 24, 25 (CRL 2474; turtle ulna?).

The reconstructed skull figured in pls. 9 and 10 (Lemoine, 1881) was dismantled, but fragments of an avian skull were found (CRL 2478, CRL 2477). Only one of the two putative bill fragments was found, but neither seems to be avian. None of the mandible is avian. Specimens in pl. 9, figs. 7–13, were identified by Lemoine (1881) as *Remiornis heberti* and the vertebra (CRL 2482, pl. 9, figs. 9–12) and the tarsometatarsus (lectotype, CRL 2481) seem to be correctly assigned. The coracoid shown in pl. 9, fig. 13a (Lemoine, 1881), most likely belongs with *Gastornis*. Plate 9, figs. 7, 8 (Lemoine, 1881) (CRL 2522; tip of mandible), are of a trionychid turtle. In pl. 10 (Lemoine, 1881), the mandible is composed of postoperculars and preoperculars of a fish, a possible turtle articular (CRL 2525), and a turtle maxilla (CRL 2524). Some of the skull bones (CRL 2477) seem to come from a large bird, but their preservation does not permit much in the way of useful comment.

ABBREVIATIONS

Institutional acronyms for specimens cited in the text are as follows: AMNH, American Museum of Natural History, New York; BMNH, British Museum (Natural History), now called the Natural History Museum, London; BR, Muséum national d'Histoire Naturelle, Paris, Mont du Berru Collection; CR, Muséum national d'Histoire Naturelle, Paris, Cernay-les-Reims Collection; CRL, Muséum national d'Histoire Naturelle, Lemoine Collection; MNHN, Muséum national d'Histoire Naturelle, Paris; L, Collection of Dr. Leve; MU, Muséum national d'Histoire Naturelle, Paris, Mutigny Collection; R, Muséum national d'Histoire Naturelle, Paris, Reims Collection; and UNSM, University of Nebraska State Museum, Lincoln.

SYSTEMATIC DESCRIPTIONS

Class Aves Linnaeus 1758

Order Gastornithiformes Stejneger 1885

EMENDED DIAGNOSIS OF ORDER. Giant ground-dwelling birds with large skulls having laterally compressed, deep bills and the articular facets of the head of the quadrates not distinctly separated by a deep groove. There is no mandibular fossa. The shoulder girdle and wing are greatly reduced with a broad, short coracoid fused to the scapula and clavicle in the adult. The tibiotarsi have low cnemial crests and a supratendinal bridge. The tarsometatarsi are short with somewhat triangular hypotarsi lacking closed canals and with two large, subequal proximal foramina. The middle trochlea of the tarsometatarsus is enlarged and more distal than the others.

Family Gastornithidae Fürbringer 1888

Genus *Gastornis* Hébert 1855

EMENDED DIAGNOSIS OF GENUS. A genus of the family Gastornithidae differing from *Diatryma* Cope 1876 by having the tibiotarsus with supratendinal bridge more proximal and central. Tarsometatarsus with middle trochlea less enlarged and outer trochlea more divergent. If R 2583 (Fig. 1) is correctly assigned to *Gastornis*, its bill is shallower (73 mm in depth) than in *Diatryma* and it also differs in having large penetrating external nares.

TYPE SPECIES. *Gastornis parisiensis* Hébert 1855; type by original designation.

INCLUDED SPECIES. *Gastornis parisiensis* Hébert 1855 and *Gastornis russelli* new species.

Gastornis parisiensis Hébert 1855

Gastornis parisiensis Hébert, 1855a:579, 1855b:1214; Owen, 1856:204; Milne-Edwards, 1867–1868:165; Fürbringer, 1888: 1178; Lydekker, 1891:357; Lambrecht, 1933:574; Brodkorb, 1967:142.

Gastornis edwardsii Lemoine, 1878:13, 1881:80, 1884:357, 1893: 353; Dollo, 1883:297; Fürbringer, 1888:1178; Lydekker, 1891: 358; Lambrecht, 1933:575; Brodkorb, 1967:142; Martin, 1983: 322.

Gastornis klaasseni Newton, 1885a:362, 1886a:349, 1886b:143, 1889:220; Fürbringer, 1888:1178; Lydekker, 1891:358; Lambrecht, 1933:576; Brodkorb, 1967:142.

LECTOTYPE. Left tibiotarsus lacking proximal end. This is the lectotype designated by Brodkorb (1967:142) and seen by him. This specimen was in the Ecole Normale Superiure, Paris, whose collections should now be in the Muséum national d'Histoire Naturelle, Paris, but I could not relocate the type. Casts of the lectotype (Fig. 2a–d) can be found in the latter museum, the Natural History Museum, London, and the University of Kansas Museum of Natural History. According to Brodkorb (1967:142), the lectotype is from the Upper Paleocene conglomerate de Meudon of the Seine-et-Oise.

REFERRED SPECIMENS. Skull fragments CRL 2477; quadrates BR 617, BR 126461, R 3561; posterior fragments of mandibles, R 3571, BR 10518; mandibular symphysis, BR 12417, BR 10512; vertebrae, CRL 2459, CRL 2463; ribs, CRL 2464, R 4154, R 3567, R 3563, R 3564, R 3565, R 3567, R 3569, R 3562, R 3566, R 3579, R 2571, BR 12737. Right scapula, coracoid and clavicle (fused), BR 45750; scapula, R 3642; coracoids, R 4151; humerus, BR 12137; radius, R 3648; pelvis, CRL 2462; partial femora, CRL 2460, BR 12420; partial tibiotarsi, CRL 2457 (lectotype *Gastornis edwardsii*), MU 12734; fibula, BR 12423; partial tarsometatarsi, CRL 2548, R 3557; two tarsometatarsi in the collection of Dr. Leve from Cernay represented as casts numbered L3092 and L3093 in the Muséum national d'Histoire Naturelle, Paris. Phalanges, CRL 2467, CRL 2465, CRL 2466, CRL 2468.

GEOGRAPHIC AND GEOLOGIC DISTRIBUTION. Upper Paleocene of France, Germany, Belgium, and England.

DESCRIPTION. The restored skull (Lemoine, 1881:pls. 9, 10) is very difficult to interpret. Much of it appears to be missing. There is an ear region that may be from a large bird. Parts of the parietals, basioccipital, and the frontal are present, but they yield no information and cannot be positively identified as avian. The putative bill near the tip is certainly the maxilla of a turtle. The fragment posterior to it cannot be found, but it is probably not avian.

The lower jaw illustrated by Lemoine (1881:pls. 9, 10) is not avian, comprising instead various parts of reptiles and fishes, including a possible soft-shelled turtle maxilla, turtle quadrate, fish preopercular, postopercular, and quadrate.

A number of isolated skull and mandibular fragments that belong to a giant bird and that can reasonably be assumed to be *Gastornis* have recently been collected. These include a partial premaxilla (R 2583) representing about one-half of the length of the bill (Fig. 1) of a small species (referred to *Gastornis* new species below). Unlike the bill of *Diatryma,* this specimen has large and penetrating external nares, and it is narrow but very deep. Judging from the figures in Sinclair (1928:pl. I, figs. 1, 2), the bill of *Omorhamphus storchii* Sinclair 1928 also has a large penetrating nostril that extended far anterad. It also appears that this form had some sort of rostral "hook." The holotype of *O. storchii* is a juvenile bird and has been synonymized with *Diatryma gigantea* (Brodkorb, 1967; Andors, 1988). It probably warrants closer comparison with *Gastornis.* The symphyseal region of the mandible of *Gastornis* (BR 12737) is preserved and has the shallow form found in *Diatryma.* The articular region of the lower jaw (BR 10512) has two large cotylae side by side and a large internal articular process. There is a large pneumatic foramen in the quadrate and a second foramen in the articular indicates that the siphuncular system was fully developed.

The entire shoulder girdle that Lemoine (1881) assigned to *Gastornis edwardsii* seems to be reptilian. The putative humeral fragments (Lemoine, 1881:pl. 8, figs. 6, 7, 23) appear to be chelonian, as does his pl. 8, fig. 15 (fibula), and pl. 8, fig. 3 (pelvis). In the same plate, figs. 1 and 10 are probably a champsosaur clavicle and fibula, respectively, and fig. 4 is a turtle pelvis. Almost all elements of the *Gastornis* shoulder girdle and wing have now been recovered, although the sternum is not present in the material that I examined. There is a beautifully preserved scapula, clavicle, and coracoid (BR 45750; Fig. 3). These elements are fused and it seems likely that the clavicles did not meet each other to form a furcula.

The scapula is elongate, broadens posteriad, and narrows anteriad so that it has a distinct neck. It is fused to a terminal scapular facet on the end of the coracoid. The glenoid fossa is hemispherical and faces dorsolaterally. Anteroventral to the glenoid fossa is a thick, blunt projection that may be a procoracoidal process. There is a large foramen facing dorsad between the brachial tuberosity and the putative procoracoid. The clavicle is flat and fused to the coracoid and the acromium of the scapula. There is a distinct foramen going into the anterior coracoid that is probably the procoracoidal foramen. The coracoid is short and broad, but it is probably not as expanded on the sternal end as in *Diatryma.*

Gastornis has reorganized the scapula and coracoid so that the scapule lies flat against the side of the rib cage. It has done this with an "L-shaped" coracoid (Fig. 3e). The anterior portion of the coracoid lies in a normal avian position with the clavicles lying across the rib cage (Fig. 3d). The coracoid is curved so

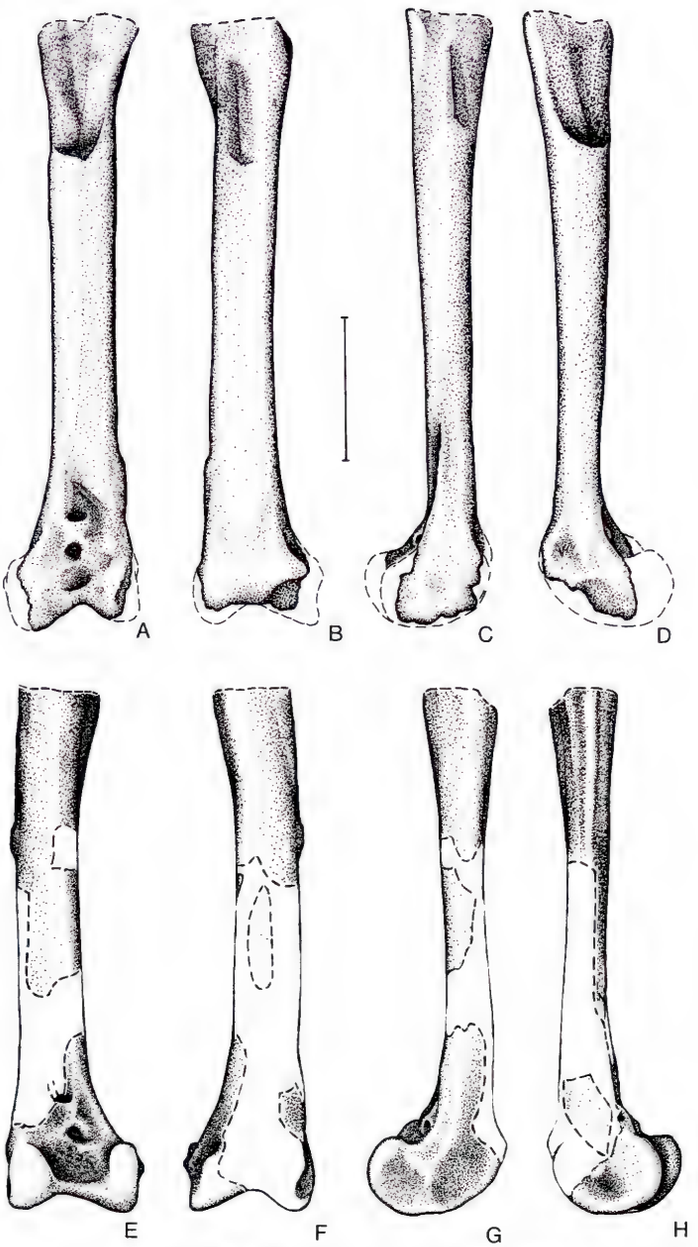

Figure 2. Tibiotarsi. **A–D.** *Gastornis parisiensis* Hébert. Holotype (right) drawn from a cast KUVP 25681, in anterior, posterior, medial, and lateral views. **E–H.** *Gastornis klaasseni* (left) BMNH A86, in anterior, posterior, lateral, and medial views. Scale bar = 10 cm.

that the scapula lies alongside of, rather than on top of, the rib cage, and the glenoid faces posterolaterad and a little dorsad (Fig. 3). This must be considered a highly derived arrangement.

The humerus is a short, robust bone (Fig. 3a, b) that is very unlike the elongate humerus restored by Lemoine (1881). The humerus has a very slight deltoid crest that curves palmad. The radius (Fig. 3c) is about one-half the length of the humerus.

The presumed ischium (Lemoine, 1881) may be correctly identified, but the "pubis" associated with it is a fish jaw with the teeth clearly illustrated. Lemoine (1881:pl. 7, figs. 4–7) depicts a caudal vertebra that is probably avian, and this is also true of the rib (Lemoine, 1881:pl. 7, fig. 10). The specimen shown as

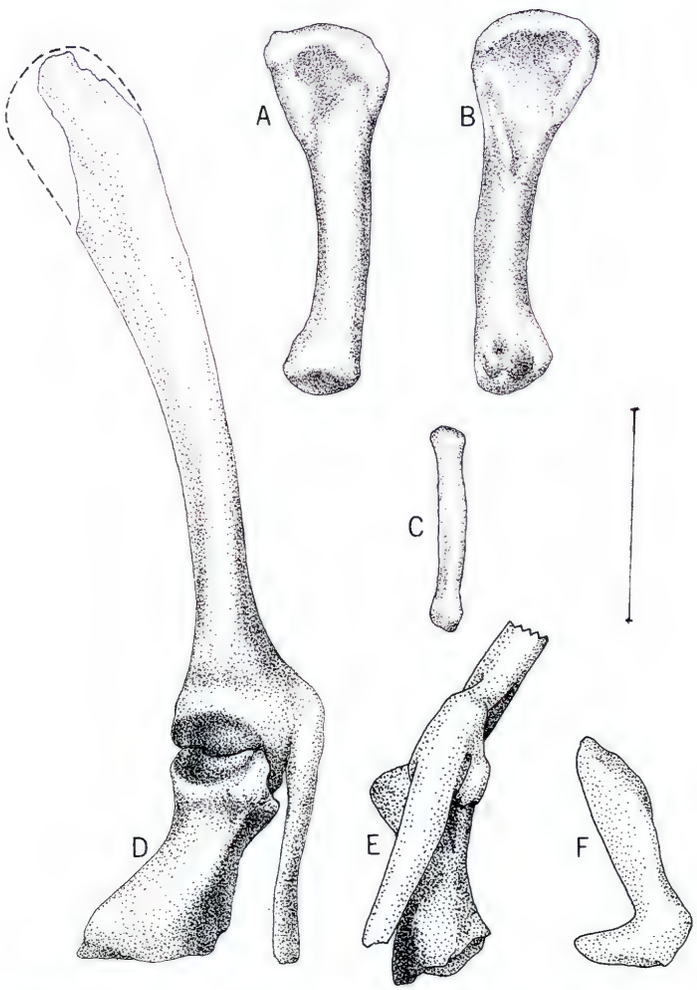

Figure 3. *Gastornis parisiensis* Hébert. **A, B.** Right humerus, BR 12137, in anconal and palmar views. **C.** Radius, R 3648. **D–F.** Right fused scapula, coracoid and clavicle, BR 45750, in lateral, anterior, and ventral views. Scale bar = 5 cm.

pl. 7, fig. 11, is non-avian, and his figs. 8 and 2 cannot be assigned with certainty.

The femur illustrated by Lemoine (1881:pl. 1, reversed) is from a species of *Gastornis,* but it may be depicted with an exaggerated length. Elongation of the femur may have been suggested by differences in shaft width of the proximal and distal ends of the shaft. If the two ends are from a single individual, practically none of the shaft should be missing and the difference in shaft diameter may have resulted from crushing.

Dollo (1883) and Newton (1886b) describe parts of the femur of *Gastornis.* As pointed out by Newton (1886a), the head and articular surface of the femur is inclined dorsad. This would have the effect of tilting the distal end of the femur away from the body. There is a large, anteriorly projecting trochanter. The outer condyle extends distinctly more distad than the inner condyle, and this tilts the tibiotarsus mediad, which helps to bring the foot back under the body. The configuration of the two joints permits a vertical posterior in a wide-bodied bird. In general, the femur of *Gastornis* is very similar to that of *Diatryma,* although the femur of *Gastornis* may have a slightly more elongated shaft.

The right tibiotarsus figured by Lemoine (1881:pl. 6, figs. 4, 5) may be the most useful element that he associated with *Gastornis parisiensis.* Lemoine's restored skeleton obviously does not represent a single species, much less a single individual, and the tibiotarsus is the most complete diagnostic bone in his material. It has a laterally situated, broad supratendinal bridge. The intercondylar space is broad and shallow. The inner condyle extends a little more anteriad than the outer condyle. The left tibiotarsus (CRL 2457) figured by Lemoine (1878:pl. 5) lacks the condyles, but it has the supratendinal bridge and enough of the proximal end to give a good impression of the length and proportions of the shaft. As it is part of the original (Lemoine, 1878) description, I here designate it the lectotype.

I have been unable to relocate the holotype of *Gastornis parisiensis.* The cast shows that it has very damaged condyles. The holotype of *G. parisiensis* is very much like that of the smaller individual referred by Newton (1886a) to *Gastornis klaasseni* (Fig. 2) from the Upper Paleocene, near Croydon, Surrey, England. I could not find features to show that *G. parisiensis* and *G. klaasseni* are specifically distinct. They both differ from *Diatryma* (Fig. 4) in having the osseous supratendinal bridge situated more proximally and centrally.

Newton (1886b) separated *Gastornis klaasseni* from *G. parisiensis* on the basis of the tibiotarsus of *G. parisiensis* having (1) a stouter shaft, (2) inner condyle not projecting as much mediad, (3) the posterior surface above the condyles flatter and broader, (4) supratendinal bridge more centrally located, (5) innercondyler depression deeper, and (6) the groove for the peroneous tendon absent. The shaft of the French specimen is a little more robust than two of the English tibiotarsi, but no more so than might be expected in a single population showing age and sex variation. Intraspecific variation may also account for the other characters except 2 and 6, which may reflect damage to the holotype of *G. parisiensis.* A more significant difference occurs between the two tibiotarsi of *G. klaasseni* (Fig. 4c, d), where in Fig. 4d the outer condyle extends farther anteriad than in Fig. 4c. All gastornithids, including *Diatryma,* have broad, well-developed supratendinal bridges and differ from both the lithornithids and *Remiornis* in this respect. In *Diatryma,* the anterior sulcus between the condyles is medial and ventral to the lower opening of the groove for m. peroneus profundus, whereas in *Gastornis* it is almost directly below that opening. The tibiotarsus seems less robust than in *Diatryma* and the outer condyle is more vertical. In lateral view, the outer condyle is rounded. In both genera, the medial condyle is elongated anteriad and inflected mediad. These last two features of the tibiotarsus probably influenced Milne-Edwards' (1867–1868) association of *Gastornis* with the Anseriformes. This viewpoint has been revived by Andors (1988; this volume).

The tarsometatarsus illustrated by Lemoine was enormously elongated by plaster restoration (Lemoine, 1878:pl. 3, figs. 1–3), and it includes fragments of a gastornithid femur and tibiotarsus. The three trochleae seem to be from one individual, but they lack contacts that establish their exact relationships with each other. Two complete tarsometatarsi of *Gastornis* collected by a private collector (Dr. Leve) from the "Region de Cernay" are represented by casts in the Muséum national d'Histoire Naturelle, Paris. These are from a large individual (L3093; total length, 303 mm) and a smaller one (L3092; total length, 267 mm). Although I was unable to examine the originals, the casts are from the best-preserved *Gastornis* tarometatarsi that I have seen and the smaller one is figured (Fig. 5a–f) to give the correct form of the *Gastornis* tarsometatarsus as it is practically uncrushed. Its proximal width is 94.5 mm and the distal width is

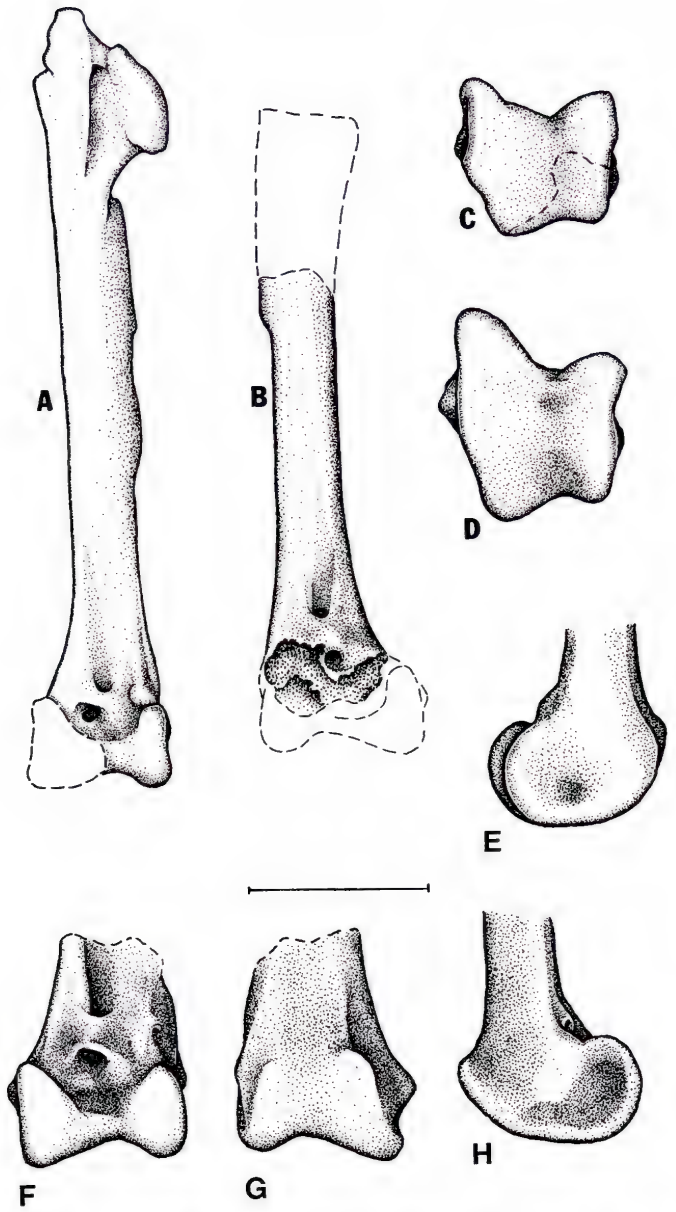

Figure 4. Tibiotarsi. **A.** *Diatryma gigantea* Cope, UNSM 49275. **B.** *Gastornis parisiensis* (syntypic series of *G. klaasseni*), anterior view. **C.** Distal end of Fig. 2E–H; **D–H.** Lectotype of *Gastornis klaasseni,* in distal, medial, anterior, posterior, and lateral views. Scale bar = 10 cm.

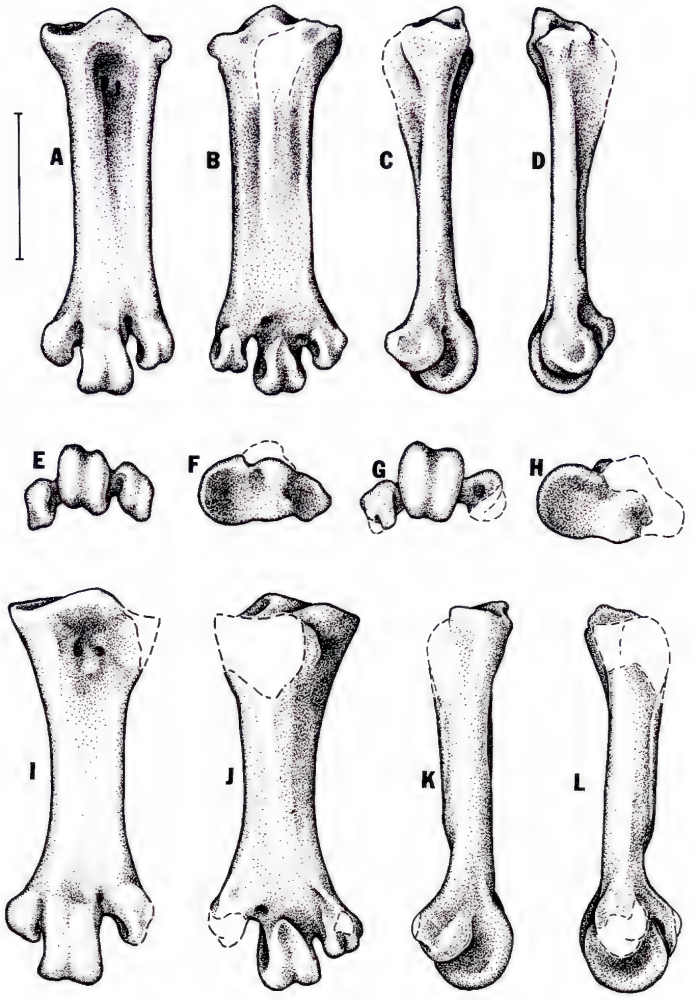

Figure 5. Left tarsometatarsi. **A–F.** *Gastornis parisiensis* (drawn from a cast, L3092, in the Muséum national d'Histoire Naturelle, Paris), in anterior, posterior, medial, lateral, distal, and proximal views. **G–L.** *Diatryma gigantea,* UNSM 49275, in distal, proximal, anterior, posterior, medial, and lateral views. Scale bar = 10 cm.

93.4 mm. Comparison of this cast with a *Diatryma* tarsometatarsus from the Eocene of Wyoming (Fig. 5g–l) shows that the middle trochlea is more enlarged in *Diatryma* and the shaft is more robust. In both cases, the tarsometatarsus is short and broad, the middle trochlea is the largest and most distal, and the intercotyler prominence is rounded. The outer trochlea is more divergent in *Diatryma* and the distal foramen is larger. The shaft of the tarsometatarsus is more constricted in the middle and the anterior groove does not extend so far distad. The hypotarsus in both genera is a simple triangular block.

DISCUSSION. The material from Croydon (referred to as *Gastornis klaasseni,* 3 individuals) all seems to be adult and it shows marked size variation (Fig. 4). Similar size variation occurs in the material from the French Paleocene.

The available skeletal material of *Gastornis* suggests that the bird was a little less than 2 m tall. Like *Diatryma,* it probably had a large head and was a predator. It was very likely an early experiment in the evolution of large terrestrial birds, and it does not have a special relationship with any modern avian group (for a contrary view, see Andors, 1988; this volume). Because of this ambiguity, I presently have not referred the Gastornithiformes to a superorder.

Gastornis minor Lemoine 1878
nomen dubium

Remiornis heberti Lemoine 1881:158, in part.
Remiornis minor Lydekker, 1891:360; Lambrecht, 1993:578; Brodkorb, 1967:141.

LECTOTYPE. Distal surface of a tibiotarsus (Lemoine, 1881: pl. 4, figs. 1–5), designated by Brodkorb (1967:141). The lectotype now appears to be lost.

AGE. Late Paleocene.

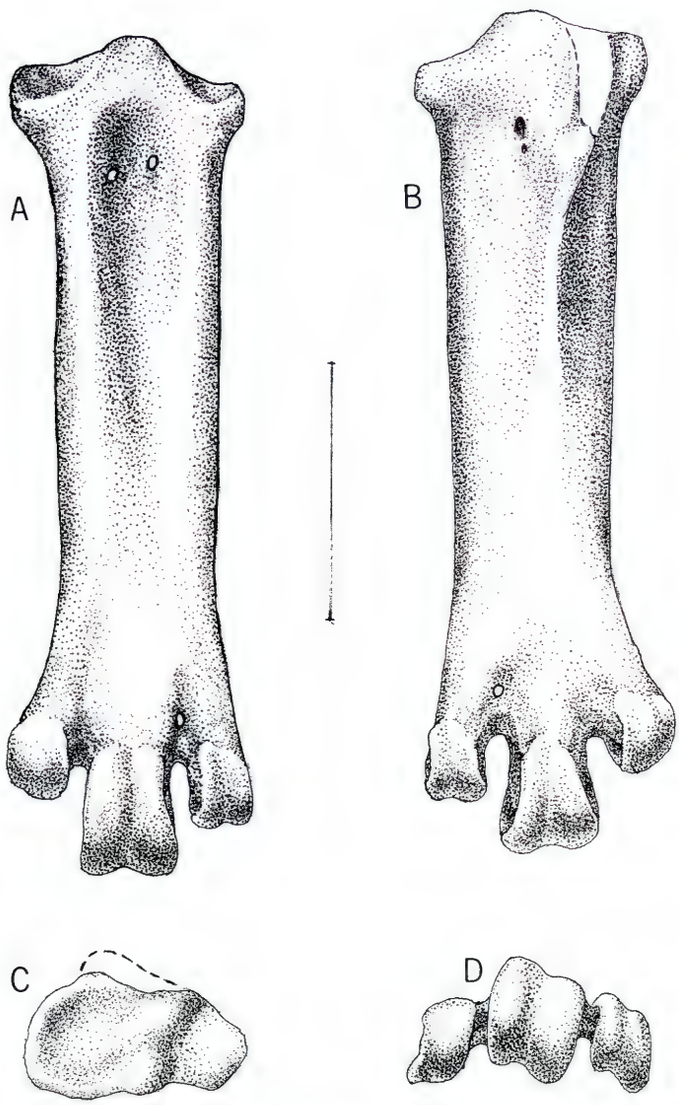

Figure 6. Holotype tarsometatarsus of *Gastornis russelli* n. sp., R 3560. **A–D.** Anterior, posterior, proximal, and distal views. Scale bar = 5 cm.

LOCALITY. Lectotype from Montchard, France; referred material from the Upper Paleocene of Berru, France.

DISCUSSION. The lectotype tibiotarsus can only be known from Lemoine's figures, and these show no diagnostic features. There is no reason to assume that the ?humerus fragment referred by Lemoine to this taxon (Lemoine, 1878:pl. 4, fig. 6) is correctly associated. It cannot be from a species of *Gastornis*, and it may not be avian.

Gastornis russelli new species

Figures 1, 5–7

HOLOTYPE. Left tarsometatarsus, R 3560, in the Muséum national d'Histoire Naturelle, Paris.

TYPE LOCALITY AND HORIZON. Berru in Reims, France, Upper Paleocene.

REFERRED MATERIAL. A bill fragment, R 2583 (Fig. 1), may belong to this species.

DIAGNOSIS. Smaller than *Gastornis parisiensis;* hypotarsal ridge extends farther distad than in all other species of *Gastornis;* middle condyle less rounded when viewed laterally than in other *Gastornis.*

ETYMOLOGY. Named for D.E. Russell, whose collecting has revitalized interest in the early Tertiary faunas of Europe.

DESCRIPTION. The tarsometatarsus (Figs. 5–7a) is short and broad, as in other species of *Gastornis,* with a broad, shallow anterior groove extending only a short distance distad. There are two widely separated proximal foramina in the anterior groove. The intercotylar process is broad and blunt. The inner and outer trochleae are at about the same level. The middle trochlea is the largest and most distal, with strongly developed condylar ridges running the length of the anterior face. The hypotarsus is a simple triangular block with poorly developed grooves. The tarsometatarsus is 129 mm long, proximal width is 31 mm, and distal width is 32 mm.

DISCUSSION. Lemoine (1878), through the description of *Gastornis minor,* suggested the existence of a small species of *Gastornis* of the sort represented by *G. russelli.* Unfortunately, the loss of the syntypic material of Lemoine's species and his mixing of this material with that of a clearly different bird in the description of *Remiornis heberti* leaves little choice except to regard *Gastornis minor* as a *nomen dubium* (Chorn and Whetstone, 1978) and to erect a new taxon for the tarsometatarsus collected by Russell.

Superorder Palaeognathae
Pycraft 1900

Order Remiornithiformes new order

DIAGNOSIS. Tibiotarsus with condyles more weakly developed than in all other orders of birds that lack an osseous supratendinal bridge; pretibial bone centrally located, short and blunt dorsally (not extended dorsad as in Struthioniformes or Rheiformes); tarsometatarsus elongate and deeply grooved anteriorly with hypotarsus triangular with two shallow medial grooves.

Family Remiornithidae new family

DIAGNOSIS. As for order.
DISTRIBUTION. Upper Paleocene of France.

Genus *Remiornis* Lemoine 1881

DIAGNOSIS. As for order.
TYPE SPECIES. *Remiornis heberti* Lemoine 1881.

Remiornis heberti Lemoine 1881

Remiornis heberti Lemoine, 1881:158 (in part); Martin, 1983: 323.

Remiornis minor Lydekker, 1891:360 (in part); Lambrecht, 1933: 578 (in part); Brodkorb, 1967:141 (in part).

LECTOTYPE. Partial tarsometatarsus, CRL 2481, in the Muséum national d'Histoire Naturelle, Paris.

Lemoine (1881) illustrates a partial tarsometatarsus (Lemoine, 1881:pl. 9, fig. 13), a coracoid (pl. 9, fig. 13), a thoracic vertebra (pl. 9, fig. 11), and a mandibular symphysis, all of which he refers to *Remiornis heberti.* The mandibular symphysis is from a trionychid turtle (Lemoine, 1881:pl. 9, figs. 7, 8). Lemoine (1881:pl. 8, fig. 23) also figures a distal end of a humerus as *R. heberti.* This specimen is lost, but it may also be from a turtle. The

vertebra (CRL 2482) and coracoid (CRL 2476) are avian, although the coracoid probably belongs to *Gastornis*. The partial tarsometatarsus (CRL 2481) can be compared directly with new material (BR 10529 and BR 12418), and I here designate it as the lectotype. Lyddeker (1891) listed only one diagnostic feature (deep anterior groove on the tarsometatarsus) for this genus, and he could only have seen this feature on CRL 2481.

TYPE LOCALITY AND HORIZON. Cernay les Reims, France; Upper Paleocene; referred material also from Mont du Berru, France, Upper Paleocene.

DIAGNOSIS. As for order.

REFERRED SPECIMENS. Dorsal vertebrae, BR 12463, BR 12454, R 3572, R 2585, CRL 2482; synsacrum, R 25181; tibiotarsus, BR 12422; tarsometatarsi, BR 10529, R 3559; middle trochlea of a right tarsometatarsus, BR 10529; left tarsometatarsus, BR 12418.

DESCRIPTION. The vertebrae include an anterior dorsal vertebra (Fig. 8d) with a well-developed hypapophysis, a slight pleurocoel, and a pneumatic foramen just above the short, stout, downturned transverse processes. The neural spine is broad and low. The posterior dorsals (BR 12463 and BR 12454) have short, triangular hypopophyses, and the one (CRL 2482) figured by Lemoine (1881:pl. 9, fig. 11) has no hypopophysis or pleurocoels. It may be the last free dorsal anterior to the synsacrum. It is heterocoelous, thereby suggesting that the entire presacral series was heterocoelous. The partial synsacrum (Fig. 8e) is very deep (arched dorsad) and flattened ventrally. It is composed of eight fused vertebrae.

The tibiotarsus (BR 12422) (Figs. 9, 10a) is long and the fibular crest terminates distally 20.5 cm proximal to the distal end. The supratendinal bridge is absent. The pretibial bone is outlined by sutures in the anterior face of the tibial shaft; it is very broad, short, and centrally located. The features of the pretibial bone correspond to McGowan's (1984) ratite condition, rather than to the narrower and more laterally placed carinate pretibial bone. It has a large, centrally placed ligamental prominence. The tendinal groove is broad and depressed just above the inner side of the ligamental prominence, and it leads laterad into a broad groove just above the inner condyle. The distal end is 33.5 mm wide and approximately 24.6 mm long anteroposteriorly.

The lectotype tarsometatarsus (Fig. 7b) is elongate and from a bird about the size of a rhea. There was a distally elongated central trochlea on the distal end and a deep anterior groove ending about 2.5 cm above the trochlea. This groove was noted by Lydekker (1891) (also in Lambrecht, 1933) as diagnostic of *Remiornis*. The facet for the first metatarsal is not evident. In these features, the lectotype tarsometatarsus agrees with two tarsometatarsi from Berru (BR 12418 and R 3559) and with a middle tarsometatarsal trochlea (BR 10529). These tarsometatarsi show that the area of the papilla for m. tibialis anterior is deeply depressed and very proximal. The proximal foramina are not clearly evident, in contrast to the condition in *Diatryma* and *Gastornis*, both of which have large penetrating proximal foramina. There is a broad intercotylar space on the proximal end that separates a round inner cotyla from the more elongated outer cotyla. The hypotarsus is solid and triangular with two hypotarsal ridges (Fig. 10). The inner ridge is short (1.5 cm) and bordered medially by the inner proximal foramen, whereas the outer ridge extends about one-third of the way down the shaft. The distal end of R 3559 is well preserved, but it is crushed laterally so that in distal view it looks more arched than it actually is. In the restoration (Fig. 10), this has been corrected to the condition seen in R 12418. The central trochlea is located farther distally than the others and the distal foramen is positioned distally. Both the inner and outer trochleae bear short flanges, and the condylar grooves are shallow. BR 3559 is 210 mm long, with a proximal width of 36 mm and a distal width of 44.5 mm.

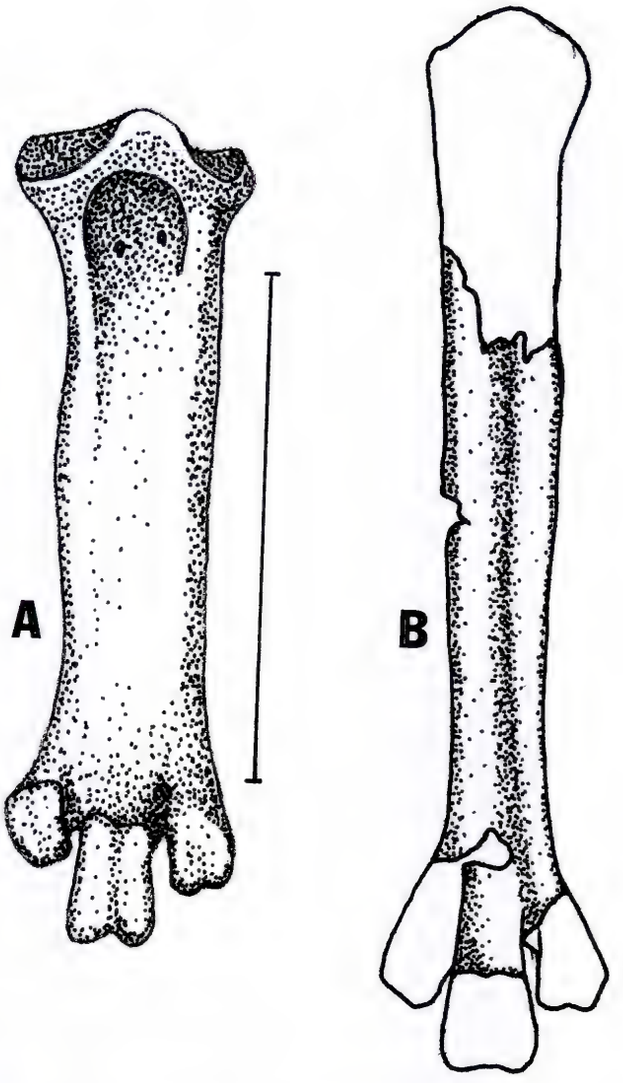

Figure 7. Tarsometatarsi. **A.** *Gastornis russelli*, R 3560, holotype. **B.** *Remiornis heberti*, CRL 2481, lectotype. Scale bar = 10 cm.

DISCUSSION. Brodkorb (1967:141) considered *Remiornis herberti* [*sic*] as a "new name for *Gastornis minor*" because the syntypic series of *G. minor* was listed with that of *R. heberti*. However, the syntypic series of *R. heberti* contains material not included in the syntypic series of *G. minor* that is diagnostic for a species of large Paleocene bird other than *G. minor*. In fact, the syntypic series of *G. minor* cannot presently be located, and the tibiotarsus fragment selected by Brodkorb as the lectotype appears to be both lost and inadequate for the assignment of additional material. *Gastornis minor* must be considered a *nomen dubium*. The removal of the lectotype of *G. minor* from the syntypic series of *Remiornis heberti* does not affect the validity of the latter name, which can now be associated with its own lectotype. The lectotype tarsometatarsus shows similarities with those of the large flightless birds commonly grouped together as "ratites."

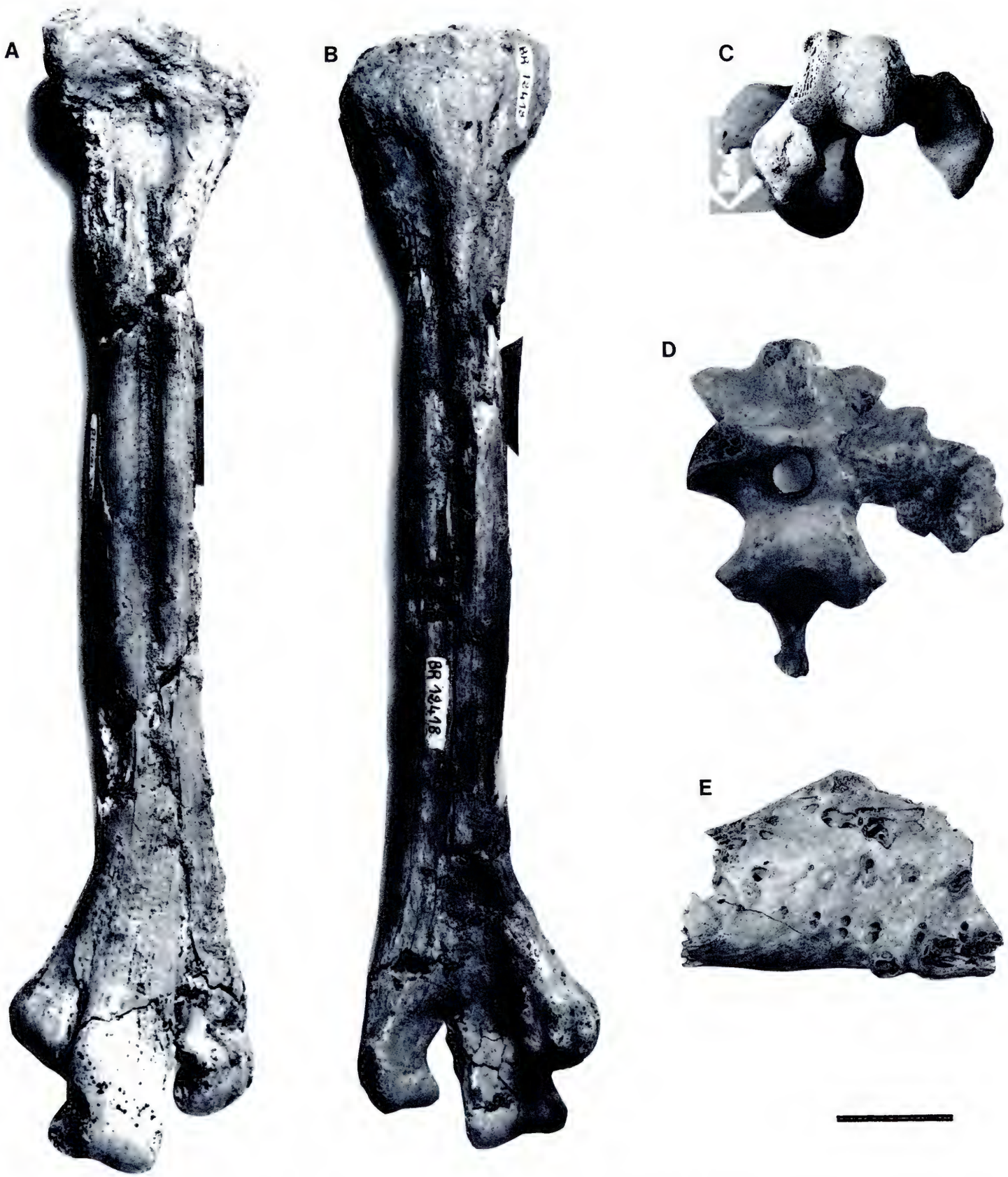

Figure 8. *Remiornis heberti* Lemoine. **A–C.** Left tarsometatarsus, BR 12418. **D.** Thoracic vertebra, R 3572. **E.** Fragment of a synsacrum R 25181. Scale bar = 5 cm.

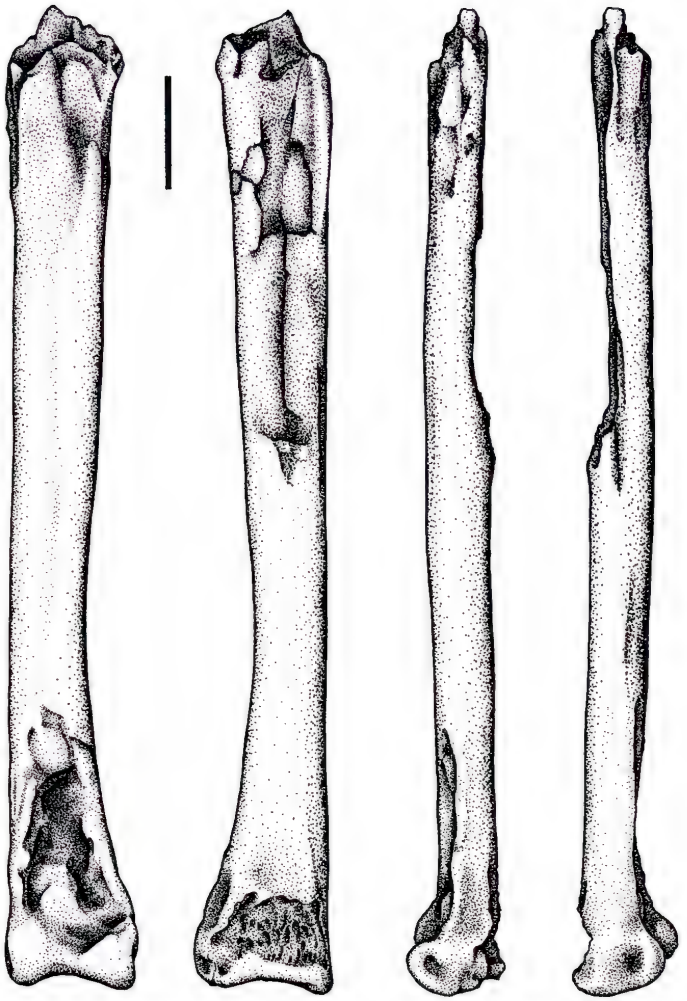

Figure 9. *Remiornis heberti* Lemoine. Right tibiotarsus, BR 19492, from left to right in anterior, posterior, lateral, and medial views. Scale bar = 3 cm.

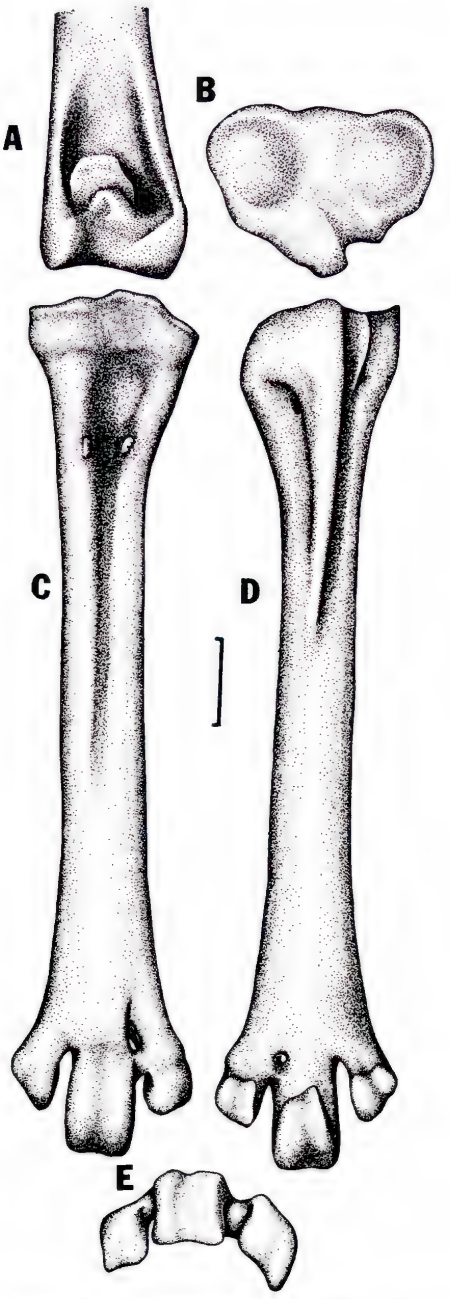

Figure 10. Restorations of the tibiotarsus and tarometatarsus of *Remiornis heberti*. **A.** Tibiotarsus based on BR 1422. **B–E.** Tarsometatarsus in proximal, anterior, posterior, and distal aspects as restored on the basis of BR 12418 and BR 3559. Scale bar = 2 cm.

The origin and evolution of ratites has been one of the most controversial subjects in ornithology. Although it has been assumed that ratites evolved from flighted ancestors, both their monophyly and relationship to other bird groups have been questioned. Cracraft (1974) argued that ratites have a Southern Hemisphere (Gondwanaland) origin and that continental drift explains their dispersal. If this is correct, we should expect to find the earliest ratites in Gondwanaland instead of Europe, and the relative sequence of phylogenetic events should correspond directly to the timing of the drift sequence. Cracraft's model requires that Africa be isolated last in the drift sequence to separate ostriches from rheas, whereas geophysicists consider the isolation of Africa to be a relatively early event (Dietz and Holden, 1970). Drift dispersal of the ostrich–rhea lineage would have had to occur during or before the Early Cretaceous, the last time of contact between these continents.

The earliest skeletal remains of putative African ratites are Eocene (*Eremopezus* Andrews 1904) and Oligocene (*Stromeria* Lambrecht 1929). Putative ratites occur in Europe (Schaub, 1940; Harrison and Walker, 1977) from the Upper Paleocene through the Middle Eocene (*Eleutherornis* Schaub 1940; *Palaeotis* Lambrecht 1928) and Lower Oligocene (*Proceriavis* Harrison and Walker 1927). Houde (1988) regards *Palaeotis* as a close relative of the ostrich. Lambrecht (1933) gives the last general review of *Eremopezus* and *Stromeria* and restudy seems warranted. South American ratites appear in the Upper Paleocene, with *Diogenornis* Alvarenga 1983 from Brazil, and possibly in the Cretaceous (Alvarenga and Bonaparte, this volume). The African forms are based on incomplete material, but they do show a widespread, early distribution of giant birds with heavily built bones that must have been flightless. Insofar as their morphology is known, it is consistent with the structure of birds normally considered to be ratites. *Remiornis* shares features with the fossil putative ratites *Mullerornis* Milne-Edwards and Grandidier 1894

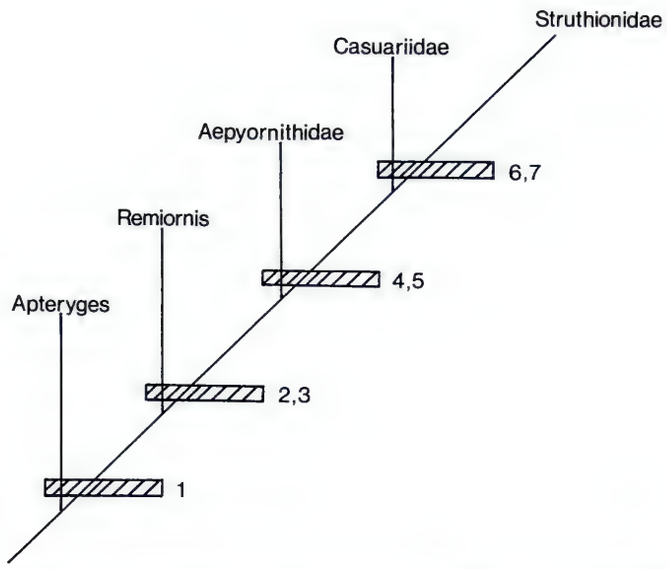

Figure 11. A cladogram of ratite birds after Cracraft (1974), showing the position of *Remiornis*. The numbered characters are (**1**) distal condyles of tibiotarsus undercut proximally by expanded intercondylar fossa, (**2**) supratendinal bridge lost, (**3**) anterior metatarsal groove deep, (**4**) internal condyle with deep ligamental pit, (**5**) internal ligamental prominence almost plate-like, (**6**) ligamental prominence completely plate-like, and (**7**) large, medially situated hypotarsal groove.

(Pleistocene of Madagascar), *Eremopezus* (Eocene of Africa), and *Stromeria* (Oligocene of Africa). The latter three genera are often placed in the Aepyornithiformes with the elephant-birds (Brodkorb, 1963).

The tibiotarsus of *Remiornis* (Figs. 9, 10) compares best with that of *Eremopezus*, and it has the external and internal condyles flattened distally. It cannot be determined whether or not the external condyle extended posteriorly as in *Struthio* Linnaeus 1758. The internal condyle of *Remiornis* does not project far anteriad, the ligamental area is not deepened, the ligamental prominence has not become plate-like, and no groove develops posterior to the prominence and the pit. The supratendinal groove is deep, a supratendinal bridge is not present, and the anterior intercondylar fossa is wide and undercuts the internal and external condyles.

Cracraft (1974) has attempted to identify primitive and derived characters in the osteology of ratites and has proposed a phylogeny. He has hypothesized that the paleognathous birds are a strictly monophyletic (holophyletic) group based on the following putative shared derived characters (Cracraft, 1974); tibiotarsus lacking a supratendinal bridge, narrow intercondylar fossa, rounded and relatively small condyles, internal condylae with no ligamental pit or plate-like ligamental prominence, and tarsometatarsus with a simple hypotarsus of one low ridge and with a shallow anterior groove. If these assumptions are correct, then we may extend Cracraft's phylogeny to include *Remiornis* (Fig. 11) between the Apteryges (moas and kiwis) and the Struthiones, placing them close to the basal stock of the elephant-birds and the ostriches, emus, and cassowaries.

CONCLUSIONS

It is now clear that the early Tertiary was a period of experimentation by birds in the evolution of large terrestrial forms. It

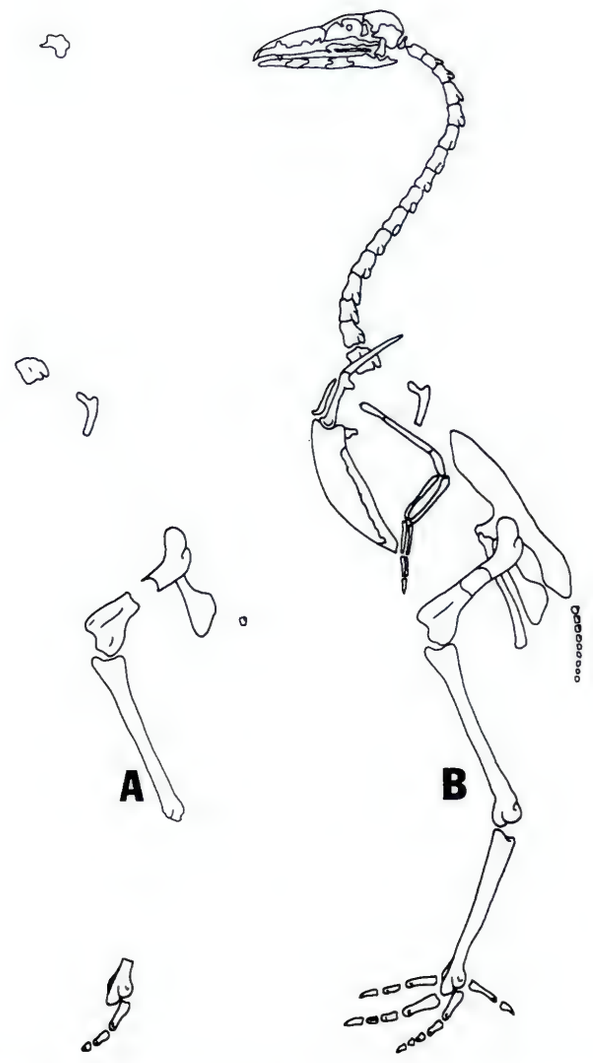

Figure 12. *Gastornis edwardsii.* **A.** Correctly identified avian material in Lemoine's (1881) restoration. **B.** Lemoine's restoration.

also seems likely that most of the modern ratites have their origins at this time. The extinction of the dinosaurs and the small size of the early mammals reduced the threat to ground-nesting birds and probably made possible an increased avian expansion into terrestrial habitats. The most spectacular of these experiments resulted in the Gastornithiformes, but many other large ground-nesting birds, including the gruids, may have originated or radiated at this time.

The gastornithiforms show a mixture of primitive and derived traits. Their palates are unusual, unlike those in the order Gruiformes. I cannot find any derived characters except those related to large size and loss of flight that unite gastornithids and gruids. Andors (1988) presented an argument that *Diatryma* is closely related to the Anseriformes, but the detailed evidence for this argument remains to be published (see Andors, this volume). I consider the gastornithid birds (including *Diatryma*) as members of an early avian radiation recognizable at the ordinal level that is now extinct.

Until recently, the only general restoration of a *Gastornis* skeleton was that of Lemoine (Fig. 12B). We can now see that only a small portion of that restoration was actually based on

Gastornis (Fig. 12A). We can also see that *Gastornis* and *Diatryma* are very similar osteologically and that the identification of *Diatryma* in Europe should be approached with caution.

The specific diversity of gastornithids does not seem to be very great, at least on the basis of skeletal material presently available. Taking into account interspecific size variation, only two species of *Gastornis* (*G. parisiensis* and *G. russelli*) seem to be present in the Paleocene of Europe.

Zhongyuanus xichuanensis Hou 1980 is based on a distal end of a tibiotarsus of a bird close to the size of *Gastornis parisiensis*. *Zhongyuanus* resembles *Gastornis* more than it does *Diatryma*, and the diagnostic features listed by Hou for *Zhongyuanus* can be duplicated in the tibiotarsi referred to *Gastornis*. There may be other features separating *Z. xichuanensis* from *G. parisiensis*, and until I have either examined the holotype or a good cast of it, I cannot resolve the taxonomic position of *Zhongyuanus*.

Remiornis may be easily separated from the gastornithids by the absence of the osseous supratendinal bridge on the tibiotarsus. The bridge is a neomorph structure of advanced birds and is formed by a medial extension of the pretibial bone (Martin et al., 1980; Martin, 1987). Almost all Mesozoic birds lack an osseous supratendinal bridge, as do all possible avian outgroups. Its presence is definitely a derived character within birds, but the absence of the bridge in a few groups like owls and parrots may be a secondary loss or reversal. The situation is even more unclear for ratites, where most forms lack the bridge. Cracraft (1974) has argued that this is a secondary loss and that ratites lacking a bridge are more derived in that respect than forms (emus, cassowaries, moas, and kiwis) retaining the bridge. The first taxa with a supratendinal bridge to appear in the fossil record are the Late Cretaceous (Maestrichtian) graculavids (Martin, 1987), which are generally considered charadriiforms. If ratites primitively lacked an osseous supratendinal bridge, they must have split off the main line of avian evolution before the Late Cretaceous. Even then their roots would lie with small birds having well-developed powers of flight. The Lithornithidae (Houde, 1988) may have been little modified survivors of that early split.

ACKNOWLEDGMENTS

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REAPPRAISAL OF THE EOCENE GROUNDBIRD *DIATRYMA* (AVES: ANSERIMORPHAE)

Allison Victor Andors

ABSTRACT. Groundbirds of the family Diatrymidae are known from the Lower Eocene (Wasatchian/Ypresian) of New Mexico, Colorado, Wyoming, New Jersey, Ellesmere Island, and France and from the Middle Eocene (Geiseltalian/Lutetian) of Germany. The disjunct distribution of these flightless giants is attributable to an episode of trans-Atlantic dispersal across a northern terrestrial corridor during the Early Eocene. One diatrymid genus (*Diatryma*) containing two Old World (*D. sarasini, D. geiselensis*) and two predominantly New World (*D. gigantea, D. regens*) species is tentatively recognized. Pelvic limb characters demonstrate a close relationship between *Diatryma* and *Gastornis* of the European Paleogene and justify including *Diatryma* in the Gastornithiformes, where it had previously and speculatively been considered to belong. Other skeletal features indicate that the broader affinities of *Diatryma* lie with the Anseriformes (Anserimorphae) and not with the Gruiformes, as formerly maintained. Against the widespread view of diatrymids as cursorial predators, it is argued that *Diatryma* was primarily herbivorous and probably incapable of sustained rapid running. Its wings were reduced distally in association with flightlessness, herbivory, and evolutionary increase in body size.

Key words: *Diatryma,* Anserimorphae, herbivory, flightlessness, gigantism, paleobiogeography.

INTRODUCTION

For the past 70 years, *Diatryma* Cope 1876 (Diatrymidae) of the Eocene of Holarctica has been widely considered a member or ally of the order Gruiformes, distantly related to the Recent seriemas (Cariamidae) of South America. This hypothesis originated with W.D. Matthew and W. Granger (1917), who refuted the nineteenth-century notion of an alliance with ratites (Palaeognathae; Cope, 1876) and described the first largely complete skeleton of this ponderous, ostrich-sized bird. For an even longer period, beginning with the earliest discovery of the genus in North America (Cope, 1876), it has been held that *Diatryma* is closely related to, if not congeneric with (Coues, 1884), the equally large *Gastornis* Hébert 1855 (Gastornithidae) from the Paleogene of Europe (Martin, 1983). In various popular works, *Diatryma* has been depicted as a necrophage (Lanyon, 1963: 10), as an herbivore (Watson, 1976), or, more typically, as a cursorial predator, or "terror crane" (Kurtén, 1972:48), analogous to the gigantic Phorusrhacidae of South America (relatives of the Cariamidae) and to carnivorous bipedal dinosaurs. It has also been suggested that following the Cretaceous extinction of the dinosaurs, diatrymids and phorusrhacids invaded the bipedal carnivore niche and stood poised to inherit the earth, thus preempting the mammals (Romer, 1966; Desmond, 1976; Marshall, 1977, 1978; Feduccia, 1980; Gould, 1986).

In a recent review of North American diatrymids (Andors, 1988), I derived a picture of *Diatryma* that is vastly different from the conventional one promulgated in ornithology textbooks for the past 100 years. It therefore seems appropriate to present here a summary reappraisal of *Diatryma.*

MATERIALS

Specimens cited herein are distinguished by the following acronyms: AMNH, Department of Vertebrate Paleontology, American Museum of Natural History, New York, New York; AMNH Orn., Department of Ornithology, American Museum of Natural History, New York, New York; FMNH, Field Museum of Natural History, Chicago, Illinois; JMB, private collection of J.M. Bowles, University of Colorado Museum, Boulder, Colorado; LACM, Natural History Museum of Los Angeles County, Los Angeles, California; NMC, National Museum of Natural Sciences, Ottawa, Canada; ROM, Royal Ontario Museum, Toronto, Ontario, Canada; UCMP, Museum of Paleontology, University of California, Berkeley, California; UM, Museum of Paleontology, University of Michigan, Ann Arbor, Michigan; UNSM, University of Nebraska State Museum, Lincoln, Nebraska; USGS, United States Geological Survey, Paleontology and Stratigraphy Branch, Denver, Colorado; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.; UW, The Geological Museum, University of Wyoming, Laramie, Wyoming; YPM, Peabody Museum of Natural History, Yale University, New Haven, Connecticut.

GENERAL FEATURES OF *DIATRYMA*

Some aspects of the anatomy of the Gastornithiformes, the order containing *Diatryma* and its Old World relative *Gastornis,* were established during the latter half of the nineteenth century, when fragmentary specimens of these birds were first discovered. The two genera were founded on postcranial elements that precluded direct comparison. *Gastornis* was based on a femur and tibiotarsus found in close proximity to each other in the Eocene "conglomérat de Meudon" of the Paris Basin (Hébert, 1855a, 1855b), whereas *Diatryma* was erected on the basis of a tar-

Figure 1. Right lateral view of a mounted cast of AMNH 6169, a nearly complete skeleton of *Diatryma gigantea* from the Lower Eocene of Wyoming. 1/22 natural size. Photograph courtesy of the Photographic Collection, Department of Library Services, American Museum of Natural History.

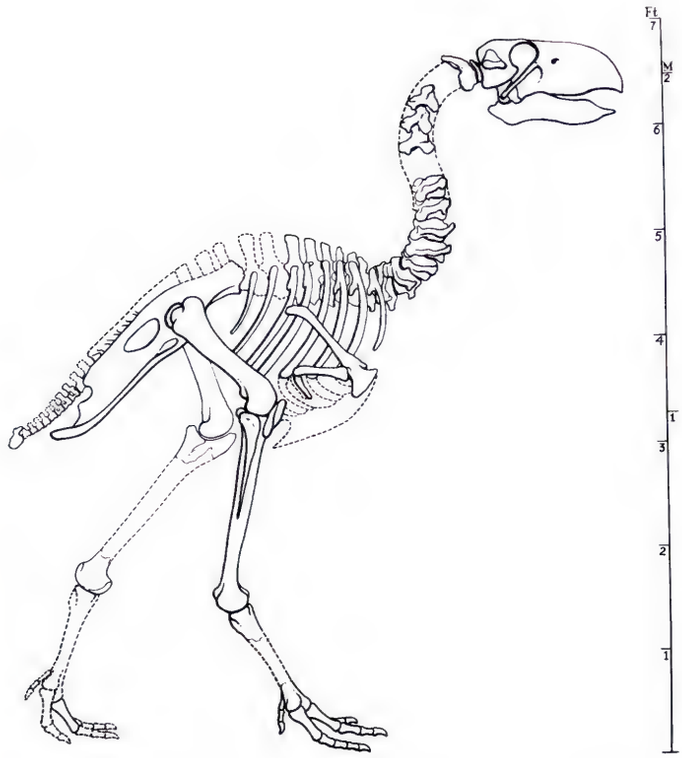

Figure 2. Reconstructed skeleton of *Diatryma gigantea* (AMNH 6169), after Matthew and Granger (1917:310, fig. 1). 1/22 natural size.

sometatarsus from the Eocene San Jose Formation of New Mexico (Cope, 1876, 1877). Only later (Milne-Edwards, 1867–1868) were tarsometatarsi of *Gastornis* reported and compared with *Diatryma* (Cope, 1876, 1877; Lemoine, 1878). Many additional elements of *Gastornis* were reported by Lemoine (1878, 1881a, 1881b, 1894), including the composite skeleton of a new species, *Gastornis edwardsii,* from the Paleocene of France. Parts of this latter reconstruction proved to be non-avian (Martin, 1983). Recognition of the similarity between *Gastornis* and *Diatryma* (Andors, 1988; Martin, this volume), which was denied by Matthew and Granger (1917), had to await restudy of the North American and European gastornithiform material.

When the first substantially complete gastornithiform skeleton (AMNH 6169; Fig. 1) came to light, Matthew and Granger referred it to *Diatryma* and published their now-classic skeletal reconstruction (Fig. 2). Their brief description of this specimen (Matthew and Granger, 1917) established the principal characters of the genus. That description and the revision of North American diatrymids by Andors (1988) provide the basis for the following generalizations about the anatomy of *Diatryma.*

Diatryma was gigantic, ground-dwelling, and flightless, with rudimentary wings and a length ratio for the humerus, ulna, and carpometacarpus of approximately 2.6:1.3:1. Adults of this genus stood about 2.1 m tall and weighed an estimated 175 kg. The skull was huge, rivalling that of the extinct Phorusrhacidae and surpassing that of all living birds, including ratites, in absolute size. The rostrum was high and laterally compressed, and the lower jaw was correspondingly deep and massive. The tip of the rostrum was only slightly decurved, and the tomia of both jaws were differentiated into sections, apparently for seizing and crushing vegetation. The cranium was broad and roofed by thick, possibly pneumatized diploë. The postorbital and zygomatic processes were fused to form hypertrophied upper temporal fenestrae, indicating that the external adductors of the lower jaw were very powerful.

The neck was short and exceedingly thick; the ribs lacked uncinate processes; the coracoid and scapula were fused end-on as in ratites; the pelvis was broad and lengthened behind the acetabulum; and the pelvic limbs were massive and moa-like in size and proportions, with a length ratio for the femur, tibiotarsus, and tarsometatarsus of 0.75:2:1. The feet were tetradactyl and anisodactyl, with a small but functional hallux, massive dorsoventrally flattened anterior toes, and a normal (and presumably primitive) avian phalangeal formula of 2–3–4–5 for tarsal digits I–II–III–IV. In general aspect, *Diatryma* resembled the flightless Takahe [*Porphyrio mantelli* (Owen 1849), Rallidae] of New Zealand, the largest extant rail, which feeds on grasses. *Diatryma* may also have been a folivore (Watson, 1976; Andors, 1988). Though a relationship of diatrymids to rails and other gruiforms has been proposed by several authors (Matthew and Granger, 1917; Brodkorb, 1967; Fischer, 1978), the resemblances between *Diatryma* and flightless rails can be ascribed to convergence. Instead, *Diatryma* and the other gastornithiforms appear to be related to the largely herbivorous order

Anseriformes, a relationship overlooked by most previous systematists (Andors, 1988).

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION

More than 50 specimens of *Diatryma* have been collected in Wyoming, Colorado, New Mexico, New Jersey, and Ellesmere Island (Cope, 1876, 1877; Marsh, 1894; Shufeldt, 1913, 1915; Matthew and Granger, 1917; Sinclair, 1928; Troxell, 1931; Wetmore, 1933; Prichinello, 1971; West and Dawson, 1978; Bown, 1979; Davidson, 1987; Rose, 1987; Andors, 1988), the majority of which were reported for the first time by Andors (1988) (Figs. 3, 4). Occurrences of *Diatryma* in the Green River and Washakie Basins of Wyoming and in the Uinta Basin and Huerfano Park of Colorado represent significant geographic range extensions for the genus. Several previously unrecognized elements, including the ulna, carpometacarpus, and first metatarsal, are present in the North American collections (Andors, 1988). By far the most productive *Diatryma* beds are those of the Willwood Formation of northwestern Wyoming (Andors, 1988) and of the Geiseltal Braunkohle of Germany (Fischer, 1962, 1967, 1978). *Diatryma* has also been reported from France (Lemoine, 1881a; Schaub, 1929; Gaillard, 1936, 1937; Brodkorb, 1967) and elsewhere in Germany (Berg, 1965) (Fig. 5).

Diatrymids are found only in the Eocene of Europe and North America. Though represented by comparatively few specimens in the Old World, *Diatryma* has a greater temporal range in Europe (Early Eocene–Middle Eocene; Ypresian–Lutetian/Geiseltalian) than in North America (Early Eocene; Early Wasatchian–Late Wasatchian) (Fig. 6). In North America, the known occurrences are all broadly contemporaneous (Andors, 1988) (Fig. 7).

Diatrymids are closely related to gastornithids (Martin, 1983; Andors, 1988), and synonymizing the Diatrymidae with the Gastornithidae would extend the temporal range of the Gastornithidae considerably (Fig. 6). Gastornithids (*Gastornis*) appear for the first time in the upper middle Paleocene of Germany (Weigelt, 1942). *Gastornis* occurs also in the Upper Paleocene (Thanetian/Cernaysian) of Belgium (Dollo, 1883) and France (Gervais, 1873, 1877; Lemoine, 1878, 1881a, 1881b, 1894; Milmine, 1959; Russell, 1959, 1964; Russell et al., 1966; Martin, 1983) and in the Lower Eocene (Sparnacian) of England (Newton, 1886; Harrison and Walker, 1977) and France (Hébert, 1855a, 1855b; Milne-Edwards, 1867–1868). A second putative genus of gastornithid, *Zhongyuanus* Hou 1980, is present in the Lower Eocene of China.

The geochronologic ranges of the Gastornithidae and Diatrymidae overlap in the Early Eocene, with Paleocene–Eocene gastornithids ultimately being "replaced" by Eocene diatrymids. (The apparent replacement may be a taxonomic artifact.) The Wasatchian/Ypresian appearance of flightless diatrymids in North America and Europe can be interpreted provisionally as a first-appearance datum that marks the establishment of a terrestrial dispersal route across the North Atlantic in the Early Eocene (Andors, 1988; see later).

TAPHONOMY AND DEPOSITIONAL ENVIRONMENTS

Diatrymids tend to be preserved by virtue of their large size and resistance to weathering or abrasion during fluvial transport. However, most specimens of these birds are extremely fragmentary. Pedal phalanges and the compact ends of long bones

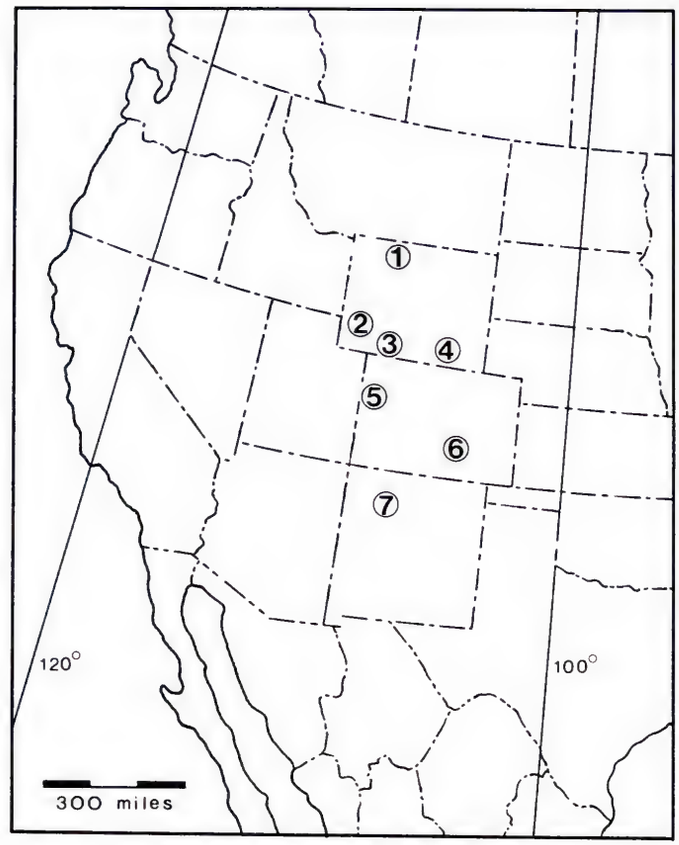

Figure 3. *Diatryma*-bearing localities in the Rocky Mountain region of western North America. See Andors (1988) for a conspectus of most known diatrymid remains from the Nearctic, including specimens of uncertain provenance (UNSM 49275; YPM 4006, 4007, uncatalogued). **1.** Willwood Formation, Bighorn and Clark's Fork Basins, northwestern Wyoming [AMNH 5166, 5167, 5917, 6169; JMB 77J5-3; LACM 6736/18200, 6882/31732, 6879/58874, 6879/58875; ROM 23671-4, 23675-81, 23682-4; UCMP 117090, 123430; UM 69964, 71824; USGS 16497, 21862, 21915, 21916, 25008, 25024, 25031 (*fide* L.M. Witmer; material not seen); USNM 12696, 12730, 13853, 15118, 256747, 256748; UW 13962, 13963, 13964, 13965; YPM 3962, 8443, 8447; YPM-PU 13106, 13258, 16336, 16349, 19516, 21770]. **2.** Wasatch Formation, Green River Basin, southwestern Wyoming [LACM (CIT) 231/57274; YPM 6352]. **3.** Wasatch Formation, Washakie Basin, southwestern Wyoming (UCMP uncatalogued). **4.** Wind River Formation, Laramie Basin, southeastern Wyoming (UW 3271). **5.** DeBeque Formation, Uinta (or Piceance Creek) Basin, western Colorado (FMNH P26824, PA27). **6.** Huerfano A Formation, Huerfano Park, southern Colorado (YPM-PU 17799). **7.** San Jose Formation, San Juan Basin, northwestern New Mexico (USNM 1120; YPM 906).

predominate in North American samples of *Diatryma* (Andors, 1988:tables 1–7), which are mostly lag accumulations. A few associated partial skeletons are known, but substantially complete individuals are exceedingly rare. Some bones appear unweathered and unabraded, suggesting rapid burial, whereas others appear partly decomposed, as if they were exposed subaerially for a long time prior to interment.

Depositional environments and associated floras and faunas indicate that the Diatrymidae were inhabitants of coastal lowlands and alluvial floodplains (Andors, 1988). Although eurytopic, diatrymids may have been primarily paludal, preferring

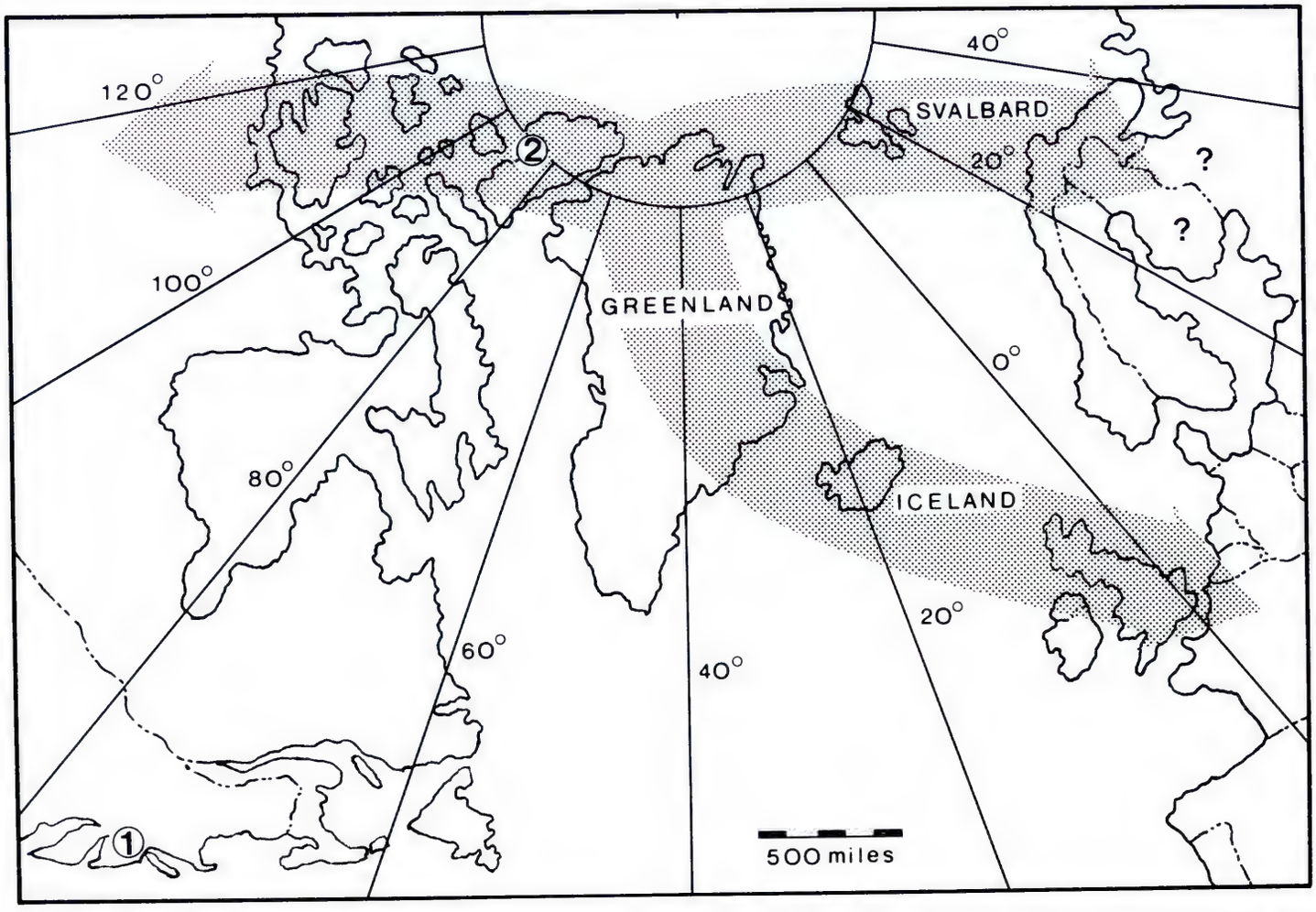

Figure 4. *Diatryma*-bearing localities and potential Early Eocene terrestrial dispersal routes in the North Atlantic region (adapted from West and Dawson, 1978:104, fig. 3). Continents and islands are shown in their present positions to facilitate recognition of geography. **1.** Manasquan or Shark River Formation, Atlantic Coastal Plain, eastern New Jersey (YPM 417). **2.** Eureka Sound Group, eastern Sverdrup Basin, west-central Ellesmere Island, N.W.T., Canada (NMC 32412).

humid, well-vegetated backswamps that were doomed to contract once the period of relative tropicality that characterized the early Tertiary came to a close. Their presumed closest relatives (Andors, 1988), the Neotropical screamers (Anseriformes: Anhimidae), exhibit similar preferences for marshy habitats. The persistence of suitable habitat in northern South America probably explains the survival of the screamers as marginal relicts. The discovery of a screamer in the Eocene of Wyoming in deposits contemporaneous with *Diatryma* (S.L. Olson, pers. comm.) demonstrates that the Anhimidae were formerly more widespread and that the gastornithiform–anseriform divergence was a pre-Eocene, early Cenozoic, or Mesozoic event.

TAXONOMY

In a departure from Brodkorb (1967), *Diatryma regens* (Marsh 1894) is removed from synonymy with *Diatryma gigantea* Cope 1876, and *Diatryma ajax* Shufeldt 1913 is placed in synonymy with the latter species. Thus, two North American species of Diatrymidae, *D. gigantea* and *D. regens*, are recognized (Andors, 1988). These differ slightly in toe proportions, phalanx 1 of digit III of *D. regens* being proportionately more slender than the corresponding element of *D. gigantea*. *Omorhamphus storchii* Sinclair 1928, a juvenile diatrymid from the Willwood Formation (Fig. 3), is interpreted as a growth stage of *Diatryma* on the basis of similarity in pelvic limb proportions (Fig. 8). It is therefore retained in synonymy with *D. gigantea*, following Brodkorb (1967). The proportionately short beak of "*Omorhamphus*" suggests potential for further growth. The size and degree of ossification of the tarsometatarsus indicate a half-grown individual 2–3 months old, extrapolating from tarsometatarsal growth patterns in the Domestic Fowl [*Gallus gallus* (Linnaeus 1758)] and in ratites (Andors, 1988:247–50).

The several European diatrymids [(?)*Diatryma sarasini* Schaub 1929; *D.* (?)*cotei* Gaillard 1936; *D.* cf. *steini* Berg 1965; *D. geiselensis* Fischer 1978] were not treated in detail in Andors (1988), but one of the named species, *D.* (?)*cotei*, was found to be utterly different from any diatrymid and therefore placed with Aves incertae sedis. These and the four currently recognized gastornithid species (*Gastornis parisiensis* Hébert 1855; *G. edwardsii* Lemoine 1878; *G. klaasseni* Newton 1886; *Zhongyuanus xichuanensis* Hou 1980) are in need of revision. Peters (1991) considers the specimen of *Diatryma* cf. *steini* from Messel, Ger-

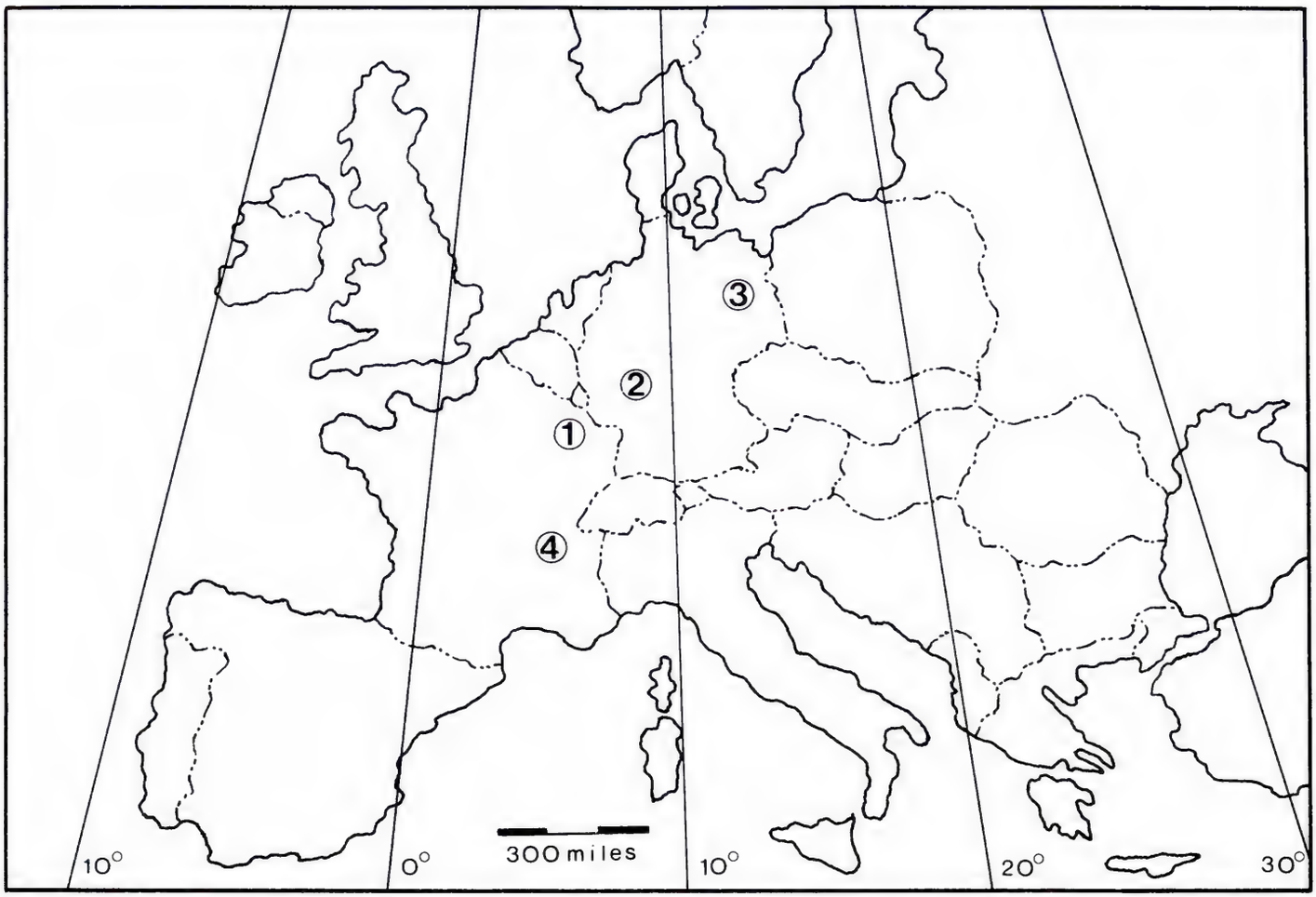

Figure 5. *Diatryma*-bearing localities in Europe. **1.** Sables à Térédines et Unios, Paris Basin, northern France (Lemoine, 1881a; Schaub, 1929; Brodkorb, 1967). **2.** Ölschiefer, Messel bei Darmstadt/Hessen, Germany (Berg, 1965). **3.** Unterkohle and Obere Mittelkohle, Geiseltal near Halle/Saale, Germany (Fischer, 1962, 1967, 1978). **4.** Gisements sidérolithiques, Lissieu (Rhône), France (Gaillard, 1936, 1937). The latter locality, called Mont-d'Or, has produced only one putative diatrymid [*Diatryma* (?)*cotei* Gaillard], here placed with Aves incertae sedis.

many, described by Berg to be, in all likelihood, conspecific with *D. geiselensis* from the Geiseltal.

RELATIONSHIP TO GASTORNITHIDAE

Twenty-five features of the pelvic limb verify the close relationship between *Diatryma* and *Gastornis* that was first postulated by Cope (1876) (Table 1). It may prove necessary to synonymize the Diatrymidae with the Gastornithidae once the latter group has been revised. Inclusion of *Zhongyuanus,* known from the distal end of a tibiotarsus, in the Gastornithidae (Hou, 1980) must be considered provisional in the absence of more complete hindlimb material. *Zhongyuanus* can be distinguished from *Gastornis* and *Diatryma* on the basis of its relatively larger lateral tibiotarsal condyle and somewhat more obliquely oriented supratendinal bridge (Andors, 1988). According to Martin (1983), *Diatryma* can be diagnosed from *Gastornis* on the basis of unspecified tarsometatarsal characters.

BROADER AFFINITIES

The history of classification of the Gastornithiformes (Diatrymidae and Gastornithidae) has been reviewed in detail by Andors (1988) and need not be repeated here. *Diatryma* has been variously considered to be related to the Palaeognathae (Cope, 1876), Psittaciformes (Andrews, 1917), Ciconiiformes (Troxell, 1931), Gruiformes (Matthew and Granger, 1917), and Anseriformes (Shufeldt, 1909; Andors, 1988). Each of these phylogenetic hypotheses may be considered briefly in turn.

PALAEOGNATHAE. The palaeognath hypothesis of gastornithiform affinities was based on the large size and structure of the proximal tarsometatarsus of *Diatryma gigantea* (Cope, 1876). Diatrymid tarsometatarsi more complete than the one available to Cope are altogether different from those of palaeognaths. Apart from gigantism, limb proportions, an obtuse coracoscapular angle, and a few other features associated with flightlessness, *Diatryma* presents no close resemblances to ratites. Its massive head and neck, neognathous palate, and extensively fused ilium and ischium would seem to preclude any near relationship to the Palaeognathae (Matthew and Granger, 1917; Andors, 1988).

PSITTACIFORMES. The several *Diatryma*-like features reported in the skulls of parrots (Andrews, 1917) are attributable to convergent evolution of herbivory (see later). These include small, sharply defined narial openings; a mobile nasal-frontal

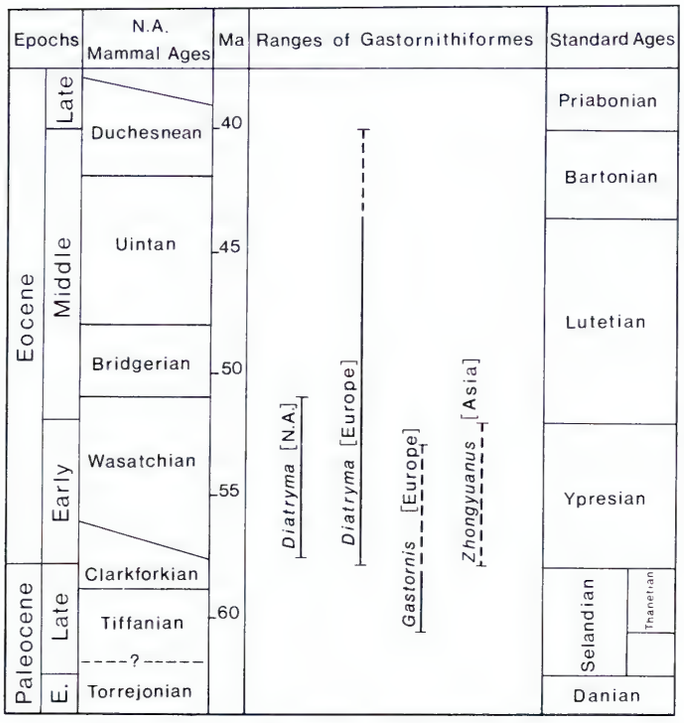

Figure 6. Geochronologic ranges of the genera of Gastornithiformes. The geochronometric scale (in Ma) and boundaries of Lyellian epochs, North American Land-Mammal Ages, and standard ages are adapted from Berggren et al. (1985). Ranges indicated by broken lines are questionable, inferred, or imprecisely known. Source: Andors (1988).

hinge; condylar, elevated jugal-maxillary articulations; simple-headed quadrates; and upper temporal fenestrae.

CICONIIFORMES. Troxell (1931) proposed that *Diatryma* was a "colossal heron" (Ardeidae), basing his opinion on the following characters that were found by him to be present in diatrymids and ardeids: holorhinal nostrils; prenarial furrows; desmognathous palate; approximation or union of the postorbital and zygomatic processes; similar mandibles; similar vertebral formulae; similar numbers of free ribs; similar orientation of the pubes; and miscellaneous similarities of the pelvic limb. As noted elsewhere (Andors, 1988), the structure of the quadrate and articular of ardeids excludes the possibility of a close relationship of this family to *Diatryma,* in which these elements are distinctive. Diatrymids have reduced or lost the posterior mandibular condyle that is retained in the quadrate of ardeids. The retroarticular processes of diatrymids are long, laterome-dially compressed, upwardly hooked structures that are radically different from the lateromedially expanded, posteriorly truncate, downwardly directed retroarticular processes of ardeids.

GRUIFORMES. An alliance between *Diatryma* and the large flightless gruiform *Phorusrhacos* Ameghino 1887 was suggested during the late nineteenth century (Gadow, 1893; Ameghino, 1895; Lydekker, 1895; Zittel, 1902), at a time when phorusrhacids were widely interpreted as ratites. Ameghino (1895) showed that the phorusrhacid quadrate had the double-headed otic process of typical carinates, and Andrews (1899) demonstrated that phorusrhacids were unrelated to ratites and were more closely related to the Recent gruiforms *Cariama* Brisson 1760 and *Chunga* Hartlaub 1860 (Cariamidae) than to any other birds. Matthew and Granger (1917) resurrected and modified the phorusrhacid hypothesis of diatrymid relationships by proposing that *Diatryma* was distantly related to *Cariama* and more remotely related to *Phorusrhacos.* According to them, the relationship to gruiforms was so distant, and the structural specialization and antiquity of *Diatryma* were so great, that *Diatryma* merited assignment to its own order (Diatrymae). Subsequent workers (Brodkorb, 1967; Fischer, 1978) took the further step of placing *Diatryma* in the Ralliformes (=Gruiformes *auct.*), with scant explanation.

In the years since 1917, the gruiform hypothesis of diatrymid affinities has been accorded a degree of acceptance out of all proportion to the quality of evidence presented. As discussed elsewhere (Andors, 1988), gruiforms differ greatly from *Diatryma* in most aspects of their skeletal anatomy. The few features advanced by Matthew and Granger as demonstrating affinity between diatrymids and gruiforms can be discounted as being either superficial (pelvic structure), derivationist (supposed derivation of the diatrymid otic process and pelvis from *Cariama*-like stages), possibly convergent (desmognathous palate), or manifestly hypothetical (supposed narrowness of the sternum). The order Gruiformes is employed as an outgroup in a phylogenetic analysis of the Diatrymidae (Andors, 1988), as summarized later.

ANSERIFORMES. R.W. Shufeldt (1909) appears to have been the first to assign *Diatryma* to the Anseres (=Anseriformes *auct.*). His Anseres included all of the gastornithiform genera then recognized. In assigning *Diatryma* to this taxon, Shufeldt was simply extending a European tradition of placing *Gastornis* and its allies in the neighborhood of waterfowl (Hébert, 1855a; Milne-Edwards, 1867–1868; Newton, 1886; Fürbringer, 1888; Beddard, 1898; Dollo, 1909). His 1909 study introduced no new facts regarding *Diatryma.* The first cladistic analysis of diatrymid relationships (Andors, 1988) showed conclusively that *Diatryma* is a sister-group of the Anseriformes. It also demonstrated a possible sister-group relationship between the Galliformes and *Diatryma* + Anseriformes. These views are summarized in Fig. 9 and Table 2.

Galliforms, *Diatryma,* and anseriforms possess a fundamentally similar mandibular articulation and suspensorium (Fig. 10), several salient features of which (characters 14b, 15b, 16b, 19b, 20b, 22b, and 23b of Table 2) are presumed to be synapomorphic. *Diatryma,* in turn, shares more features in common with the Anseriformes than with any other Recent order of birds. The resemblances among *Diatryma,* screamers (Anhimidae), and waterfowl (Anseranatidae + Anatidae) are subtle, but pervasive and apparently synapomorphic, involving features of the rostrum (2b, 3b), craniofacial hinge (4b), lacrimal (5b, 6b), bony palate (10b, 12b), quadrate (17b), mandible (21b), pectoral girdle (26b, 27b), wing (35b), pelvis (36b, 37b, 38b), and pelvic limb (41b, 42b, 43b, 44b, 45b, 46b, 47b). In keeping with its antiquity, *Diatryma* retains many features [cracid-like rostrum; holorhinal, impervious nares; zygomatic processes and upper temporal fenestrae; imperforate occiput, lacking fontanelles; a simple, abutting palatine–pterygoid articulation; sessile basipterygoid processes; unfused presynsacral thoracic vertebrae; a synsacral formula (Boas, 1933) of ca. 2 + 4 + 4 + 2 + 4 = 16; amphicoelous caudal centra; well-developed caudal hypocentra; eight pairs of free vertebral ribs; a well-developed coracoidal fenestra; a ventrally recurved deltoid crest on the humerus; a trenchant femoral neck and high, robust femoral trochanter] that appear to be primitive with respect to Anseriformes. All or most of these characters can be interpreted as galliform symplesiomorphies.

The system of relationships presented invokes homoplasy in several lineages, most conspicuously in *Diatryma* and screamers, in which there are several apparent parallelisms (thickened or-

Table 1. Postulated synapomorphies of the pelvic limb (+) shared by Diatrymidae (*Diatryma*) and Gastornithidae (*Gastornis, Zhongyuanus*).[a] Characters 1–11 apply to the femur, 12–18 to the tibiotarsus, and 19–25 to the tarsometatarsus (see legend below for details).

Taxon	Character*												
	1	2	3	4	5	6	7	8	9	10	11	12	13
Diatryma gigantea	+	+	+	+	+	+	+	+	+	+	+	+	+
Gastornis parisiensis	+	+[b]	+	?	?	?	?	+	+	?	?	+	+
Gastornis edwardsii	+[c]	+	+	+	?	+	+	+	+	+	+	+	+
Gastornis klaasseni	+[c]	+[d]	+	+	+	+	?	?	?	?	?	+	+
Zhongyuanus xichuanensis	?	?	?	?	?	?	?	?	?	?	?	+[e]	+

	Character*											
	14	15	16	17	18	19	20	21	22	23	24	25
Diatryma gigantea	+	+	+	+	+	+	+	+	+	+	+	+[f]
Gastornis parisiensis	+	+	+	+	+	?	?	?	?	+	?	?
Gastornis edwardsii	+	+	+	+	+	+	+	+	+	+	+	+
Gastornis klaasseni	+	+	+	+	+	?	?	?	?	?	?	?
Zhongyuanus xichuanensis	+	+	+	+	+	?	?	?	?	?	?	?

* Femur: **1,** shaft straight, robust; **2,** extremities proportionately wide; **3,** trochanter produced anteriorly as a very prominent crest; **4,** neck trenchant, angled proximally, slightly constricted beneath head; **5,** iliac facet overhangs posterior part of shaft as a rounded tuberosity; **6,** pneumatic foramen absent; **7,** lateral condyle projects distad considerably beyond medial condyle; **8,** lamina between rotular groove and popliteal fossa very thin; **9,** proximal end of popliteal fossa not clearly delimited; **10,** distal end of popliteal fossa overhung by a well-developed intercondylar crest; **11,** attachment for tendinous loop of m. biceps femoris a deep, circular pit. Tibiotarsus: **12,** proximal shaft convex in front and flattened behind, distal shaft semilunate in transverse section with the convexity facing posteriad; **13,** medial condyle elongated anteroposteriorly and inflected mediad; **14,** internal ligamental prominence very well developed; **15,** lateral condyle rounded, smaller in anteroposterior diameter than medial condyle; **16,** external ligamental prominence low; **17,** supratendinal bridge and groove for tendon of m. extensor digitorum longus situated toward inner side of front of shaft; **18,** anterior intercondylar fossa very wide and deep. Tarsometatarsus: **19,** trochleae splayed widely with respect to shaft; **20,** external intertrochlear notch wider and longer than internal intertrochlear notch; **21,** trochlea III larger, longer, and more anteriorly situated than trochleae II and IV; **22,** trochlea II shorter, smaller, and deflected farther posteriad than trochlea IV; **23,** trochlea IV helical in form; **24,** canalis interosseus tendineus for tendon of m. extensor brevis digiti IV a partly closed groove not roofed over by bone; **25,** foramen vasculare distale relatively distal in position and somewhat oblique, penetrating between metatarsals III and IV in a posterodistomedial direction.

[a] Compiled from the following sources: Hébert, 1855a, 1855b; Owen, 1856; Milne-Edwards, 1867–1868; Lemoine, 1878, 1881a; Dollo, 1883; Newton, 1886; Harrison and Walker, 1977; Hou, 1980; Andors, 1988.

[b] Verified for distal extremity only.

[c] Shaft incomplete.

[d] Verified for proximal extremity only.

[e] Confirmed only for distal shaft.

[f] Variable in size and in proximodistal position; absent in young birds and in some adults.

bital rims; absence of uncinate processes on the ribs; presence of an enlarged distal tubercle on the deltoid crest; cribriform anterior carpal fossa; elongate proximal metacarpal symphysis; elongate alular metacarpal; pectineal process of pubis represented by a low convexity). These parallelisms are problematical (see Andors, 1988:307–08), but they tend to reinforce the impression that *Diatryma* and anhimids are primitive within the diatrymid–anseriform assemblage. *Diatryma* exhibits intermediacy between the orders Galliformes and Anseriformes in the structure of its lacrimal, pterygoid (Fig. 10B), quadrate (Fig. 10E, H, K), retroarticular processes (Fig. 10N), humerus, and femur (Andors, 1988). Its mosaic character attests to the consanguinity of the Anseriformes and Galliformes, which was questioned by Olson and Feduccia (1980).

My views concerning the interrelationships of *Diatryma*, Anseriformes, and Galliformes are summarized by the following classification (adapted from Sibley et al., 1988:414–15):

Parvclass Galloanserae
  Superorder Gallomorphae
    Order Craciformes
    Order Galliformes
  Superorder Anserimorphae
    Order Gastornithiformes
    Order Anseriformes

Placement of the Gastornithiformes alongside the Anseriformes as sister-groups harks back to the forgotten views of several nineteenth-century naturalists (Hébert, 1855a; Milne-Edwards, 1867–1868; Newton, 1886), who considered *Gastornis* and waterfowl to be closely allied.

The large size, highly derived feeding apparatus, and reduced wing of *Diatryma* justify recognition of the Gastornithiformes as a separate order. The origin of the Gastornithiformes may be traced to an ancestral line leading to the Anseriformes, and these groups may in turn be postulated to have arisen from some progenitor of the Galliformes. The common ancestor of these orders evolved a unique but initially generalized feeding apparatus, perhaps associated originally with omnivory (as in the majority of Galliformes), but eventually giving rise to more specialized trophic adaptations, including herbivory (*Diatryma*, screamers, geese), filter-feeding (dabbling ducks), and piscivory (mergansers).

FEEDING ADAPTATIONS AND PALEOECOLOGY

The skull of *Diatryma* was prokinetic, and movements of the upper and lower jaws were apparently coupled. The feeding mechanism possessed a complex of features (high, laterally compressed, heavily ossified rostrum with steeply arched culmen; stout labial processes of the premaxillae; stout lateral nasal bars;

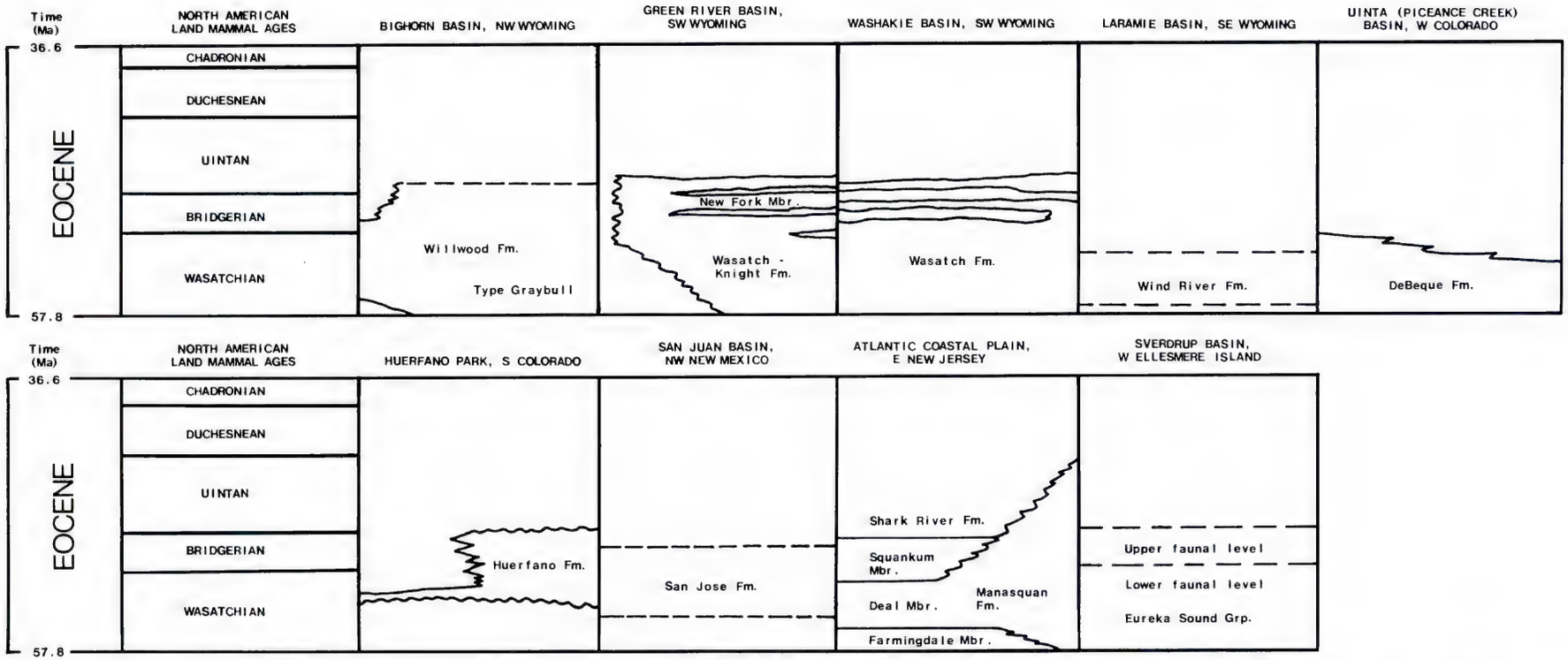

Figure 7. Correlation chart of North American *Diatryma*-bearing sediments, showing estimated ages (in Ma) of epoch boundaries (Berggren et al., 1985), standard North American Land-Mammal Ages, and interpreted stratigraphic positions of all North American formations in which *Diatryma* has been found. The known temporal range of *Diatryma* in North America is approximately Early Wasatchian to Late Wasatchian. Previously reported Clarkforkian and Bridgerian occurrences of this genus in the New World (Brodkorb, 1967; Baird, 1967) are now considered to be Wasatchian in age (Rose, 1981; Andors, 1988). Source: Andors (1988).

restricted nares; well-developed nasal-frontal hinge; condylar jugal–maxillary articulations; massive mandible with elongate, slender symphysis and deep rami; rostral and mandibular tomia differentiated into an anterior seizing/cropping region and a posterior slicing/crushing region) interpreted as adaptations for folivory and paralleled in part by Recent avian folivores (including the largest rail, *Porphyrio mantelli*, and the largest parrot, *Strigops habroptilus* G.R. Gray 1845), which have likewise lost or reduced their capacity to fly and have undergone correlated increase in body size. Against the received view of diatrymids as cursorial predators (Heilmann, 1926; Simpson, 1950; Romer, 1966; Desmond, 1976; Feduccia, 1980; Gould, 1986), it can be argued that the weakly developed rostral hook, reduced flexor tubercles on the claws of the toes, and shortened tarsus seriously impeded this mode of feeding and may have precluded it altogether. The folivore hypothesis (Watson, 1976; Andors, 1988) best fits the known morphology of the diatrymid jaw apparatus, and it agrees also with the large size, flightlessness, neck and pelvic limb proportions, vegetated paleoenvironment, and presumed anseriform affinities of these singular birds.

FLIGHTLESSNESS, GIGANTISM, AND LOCOMOTORY ADAPTATIONS

Folivory and flightlessness are evolutionarily related in some birds (Morton, 1978; Andors, 1988; Grajal et al., 1989). Leaves require a long retention time for the extraction of nutrients, and they must be eaten in bulk and accommodated by a large storage space in the alimentary canal to be utilized efficiently. The added weight, long retention time, and slow nutrient release of a diet of leaves are disadvantageous to a flying animal. Birds that subsist on leaves have, accordingly, tended to forfeit the energetic expense of flight and evolved large size. Cases in point are *Diatryma* and folivorous rails (*Porphyrio mantelli*) and parrots (*Strigops habroptilus*) that are the largest representatives of their kind (Andors, 1988).

With loss of flight capability and increase in body weight, the wings of birds undergo a reduction in relative length. Wing reduction can be a secondary consequence of phyletic body size increase and may not necessarily be a product of selection for reduced wings *per se* (Andors, 1988). Reduction or loss of wings and wing muscles tends to move the center of mass posteriad, and compensatory adaptations concerned with the maintenance of balance are therefore required (Alexander, 1983a). Cursorial ratites have compensated for the disturbance to balance resulting from the reduction of the wings by narrowing and lightening the posterior part of the trunk. *Diatryma*, moas, and elephant-birds, which retain a wide pelvis (Lowe, 1930), have instead shortened the tarsometatarsus to bring the foot under the new center of mass.

The composite bony wing length of *Diatryma* (31 cm) is comparable to that of a flying bird weighing a few kilograms or less. An adult *Diatryma* is judged to have weighed approximately 175 kg (Andors, 1988), based on the scaling relationship between least shaft circumference of the tibiotarsus and live body weight in Recent birds (Campbell and Tonni, 1983). From the disproportion between the diatrymid wing and body, it is evident that the wing has diminished in relative length while body size has increased. From transformation series of Pseudosuchia + Theropoda (Fig. 11:1–7) and Anseriformes + Gastornithiformes (Fig. 11:8–13), it can be inferred that *Diatryma* arose from volant stock possessing wings of the approximate dimensions of flighted anseriforms, in which the wings are proportionately four times longer than in the fossil. In both clades

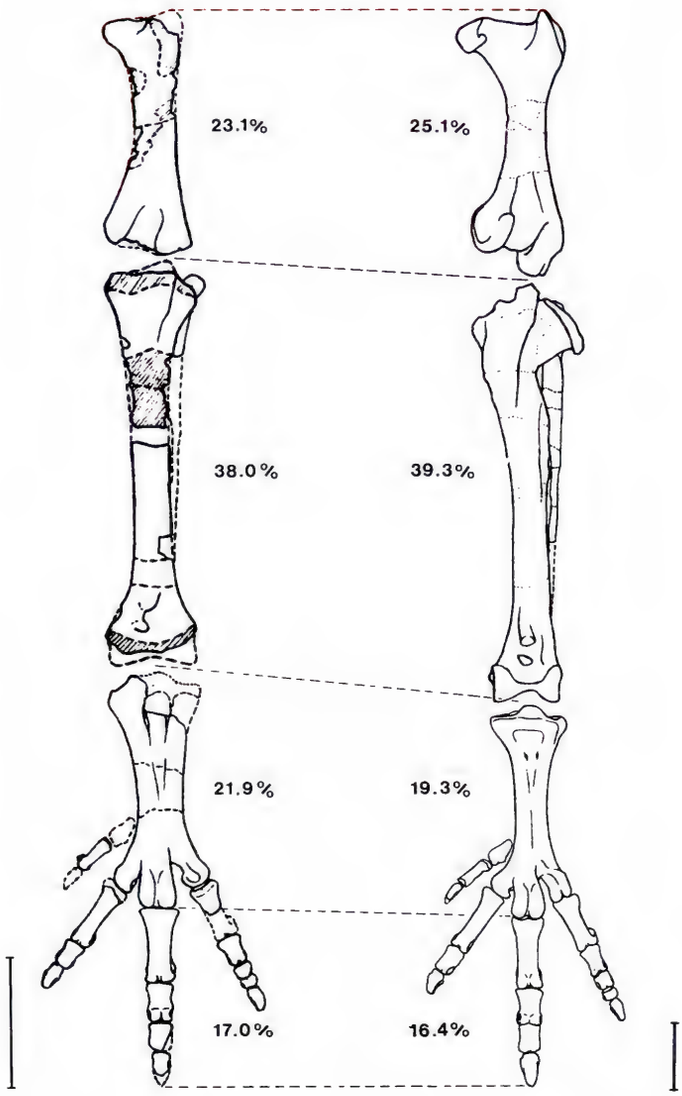

Figure 8. Reconstructed left pelvic limbs of (left) *Omorhamphus storchii*, an immature diatrymid [YPM-PU 13106, holotype: left leg with shaft of tibiotarsus restored (Sinclair, 1928)], and of (right) *Diatryma gigantea*, represented by a composite of two adults [AMNH 6169: left femur, right tibiotarsus (reversed), right fibula (reversed); YPM-PU 16336: left tarsometatarsus, left digits I–IV]. The limbs are shown in anterior view and are drawn to the same absolute length to demonstrate the similar intramembral proportions (given in approximate percentages) and probable conspecificity of these taxa. Each scale bar = 10 cm.

of obligate bipeds, and in flightless representatives of the Gruiformes and Columbiformes (Andors, 1988), the distal forelimb segments have convergently undergone progressive reduction in relative length with increasing body size. The end-members of the two series shown here (*Tarbosaurus* Maleev 1955b and *Diatryma*) have proportionately the shortest limbs and are truly gigantic. The vestigial wing of *Diatryma* has been reduced to about the same proportion as in kiwis (*Apteryx* Shaw 1813), emus (*Dromaius* Vieillot 1816), and extinct flightless geese (*Thambetochen* Olson and Wetmore 1976) (Andors, 1988).

The hindlimb proportions of *Diatryma* approach those of various graviportal birds, including kiwis (*Apteryx*), moas

Table 2. Matrix of character-states of taxa included in an analysis of the affinities of *Diatryma* (Fig. 9). Polarity codes: a, primitive; b, c, derived with respect to a. See Andors (1988) and legend below for an analysis of the numbered characters (1–47) and the hypothesized polarity transformations among them (a–b, a–b–c). Abbreviations: G, Galliformes; D, *Diatryma*; Anh, Anhimidae; Ans, Anseranatidae; Ana, Anatidae.

	Characters and character-states*																							
Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
G	a	a	a	a	a	a	a	a	a	a	a	a	a	a, b	b	b	a	a	b	b	a	b	a, b	b
D	a	b	b	b	b	b	b	a	a	b?	a	b	a	b	b	b	b	a	b	b	b	b	b	a
Anh	b	a	a	b	b	b	b	b	a	b	a	b	b	b	b	b	b	b	b	b	b	b	b	a
Ans	b	b	b	b	c	b	a	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	a
Ana	b	b	b	b	c	b	a	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	a

	Characters and character-states*																						
	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47
G	a	a	a	b	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
D	b?	b	b	a	a	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b
Anh	b	b	b	a, b	b	b	a	b	b	b	b	b	b	b	a	b	b	b	b	b	b	b	b
Ans	a	b	c	a	b	a	a	a	a	a	b	b	b	b	a	a	b	b	b	b	b	b	b
Ana	a	b	c	b	b	a	b	a	a	a	b	b	b	b	b	a	b	b	b	b	b	b	b

* **1,** Nasal septum: (a) imperforate; (b) perforate. **2,** External nares: (a) elongate; (b) restricted to a posterior position. **3,** Premaxilla, labial process: (a) slender; (b) very deep. **4,** Nasal-frontal hinge: (a) an indistinct zone of flexion; (b) a distinct, transverse crease. **5,** Lacrimal, head: (a) usually joined to lateral nasal bar; (b) moderately developed, situated beneath nasal-frontal hinge; (c) usually large, only entering nasal-frontal hinge at its anterior end. **6,** Lacrimal, descending process: (a) poorly developed and pointed distally or elongate and broadened distally, bracing or approaching jugal bar; (b) variable in length and width, but typically short, broadened, and forked distally, projecting freely into antorbital vacuity without bracing or approximating the jugal bar. **7,** Orbital rims: (a) relatively thin; (b) conspicuously thickened, forming orbital crests. **8,** Zygomatic process: (a) more or less well developed, fusing with postorbital process to form a proportionately small or hypertrophied upper temporal fenestra; (b) absent or vestigial, the temporal fossa being reduced to a ventrally facing pocket situated behind the orbit, medial to the postorbital process. **9,** Occipital fontanelles: (a) absent; (b) present. **10,** Bony palate: (a) schizognathous; (b) desmognathous. **11,** Pterygoid–palatine articulation: (a) a simple abutment or peg-and-socket arrangement; (b) a ball-and-socket joint involving two extensions of the pterygoid. **12,** Pterygoid, basipterygoid (parasphenoid) articulation: (a) anterior in position; (b) medial in position, forming a prominent, longitudinally extensive flange. **13,** Parasphenoid, basipterygoid processes: (a) sessile, not distinctly set off from rostrum; (b) almost pedicellate, clearly set off from rostrum. **14,** Quadrate, otic process: (a) with wide incisure; (b) with narrow or obsolete incisure, forming a more or less unitary joint ball. **15,** Quadrate, process for origin of m. adductor mandibulae externus profundus: (a) absent; (b) present. **16,** Quadrate, mandibular condyles: (a) three in number, forming a V-shaped configuration; (b) two in number, separated by a shallow intercondylar sulcus and forming a bilobate, peanut-shaped configuration in which the lateral condyle is larger and more bulbous than the medial condyle. **17,** Quadrate, medial mandibular condyle: (a) rounded, truncated medially, directed medially or somewhat posteromedially with respect to lateral condyle; (b) compressed anteroposteriorly and elongated in an anteromedial direction. **18,** Quadrate, posterior buttress for jugal bar: (a) small, represented by a low ridge or swelling; (b) large, equalling or surpassing the lateral mandibular condyle in volume. **19,** Mandible, articular fossa: (a) V-shaped; (b) bipartite, inclined posteriorly, with the axes of the lateral cotyla, crista intercotylaris, and medial cotyla parallel to one another and directed anteromedially. **20,** Mandible, lateral mandibular process: (a) [primitive condition unknown]; (b) rounded and prominent laterally, projecting abruptly from the ramal axis and forming approximately a right angle with the retroarticular process. **21,** Mandible, medial mandibular process: (a) spike-like, tapered distally, not furnished with a distinct anterior or anterodorsal facet; (b) expanded distally and flattened or faceted anteriorly or anterodorsally. **22,** Mandible, retroarticular processes: (a) absent or poorly developed; (b) long, upwardly curved. **23,** Mandible, retroarticular processes: (a) slender and rounded, rarely laterally compressed and blade-like; (b) laterally compressed and blade-like. **24,** Caudal vertebrae, hypocentra: (a) well developed; (b) poorly developed. **25,** Ribs, uncinate processes: (a) present; (b) absent. **26,** Coracoid: (a) elongate, slender, with narrow base; (b) relatively short, broad-based. **27,** Coracoid, sternocoracoidal process: (a) low to somewhat convex; (b) very prominent, truncated squarely at tip; (c) very prominent, the superior angle being produced far laterally. **28,** Coracoid, coracoidal fenestra: (a) present; (b) absent. **29,** Humerus, deltoid crest: (a) recurved in a palmar direction; (b) not recurved. **30,** Humerus, deltoid crest: (a) without a prominent tubercle near its distal end; (b) with a well-developed distal tubercle. **31,** Radius: (a) without a distal, external crest; (b) with an elongate distal, external crest. **32,** Carpometacarpus, anterior carpal fossa: (a) noncancellous; (b) cribriform. **33,** Carpometacarpus, proximal metacarpal symphysis: (a) proportionately short; (b) relatively elongate. **34,** Carpometacarpus, alular metacarpal (II): (a) proportionately short; (b) relatively elongate. **35,** Carpometacarpus, minor metacarpal (IV): (a) bowed posteriorly away from the major metacarpal (III); (b) almost straight and oriented parallel to the major metacarpal (III). **36,** Pelvis, renal fossa: (a) deep; (b) shallow. **37,** Pelvis, caudal iliac crest: (a) well developed; (b) moderately developed or obsolete. **38,** Pelvis, iliac recess: (a) deep or moderately deep; (b) absent or only moderately developed. **39,** Pelvis, ischiadic fenestra(e): (a) absent; (b) present. **40,** Pelvis, pectineal process: (a) more or less prominent; (b) represented by a low convexity. **41,** Femur: (a) without marked posterior divergence of the medial and lateral condyles; (b) with the condyles diverging posteriorly to a marked degree. **42,** Tibiotarsus, medial condyle: (a) without marked anteroposterior elongation; (b) with extreme anteroposterior elongation. **43,** Tibiotarsus, medial condyle: (a) not or only slightly inflected medially; (b) inflected strongly medially. **44,** Tibiotarsus, intercondylar incisure: (a) relatively narrow; (b) very wide. **45,** Tarsometatarsus, intercondylar prominence: (a) relatively narrow, acutely domed; (b) broad, bulbous. **46,** Tarsometatarsus, hypotarsus: (a) squarish; (b) typically oblong. **47,** Tarsometatarsus, inner condyle of outer trochlea (IV): (a) not produced anteriorly; (b) produced anteriorly.

(*Anomalopteryx* Reichenbach 1852), elephant-birds (*Mullerornis* Milne-Edwards and Grandidier 1894, *Aepyornis* Geoffroy-Saint-Hilaire1851), and dodos (*Raphus* Brisson 1760), possibly implying similar locomotory abilities and posture (Andors, 1988).

It is unlikely that *Diatryma*, with its proportionately short tarsometatarsus, could have run as rapidly as cursorial ratites, in which the distal segment of the leg is relatively elongated. The massive, elongate femur, short tarsometatarsus, and rather short,

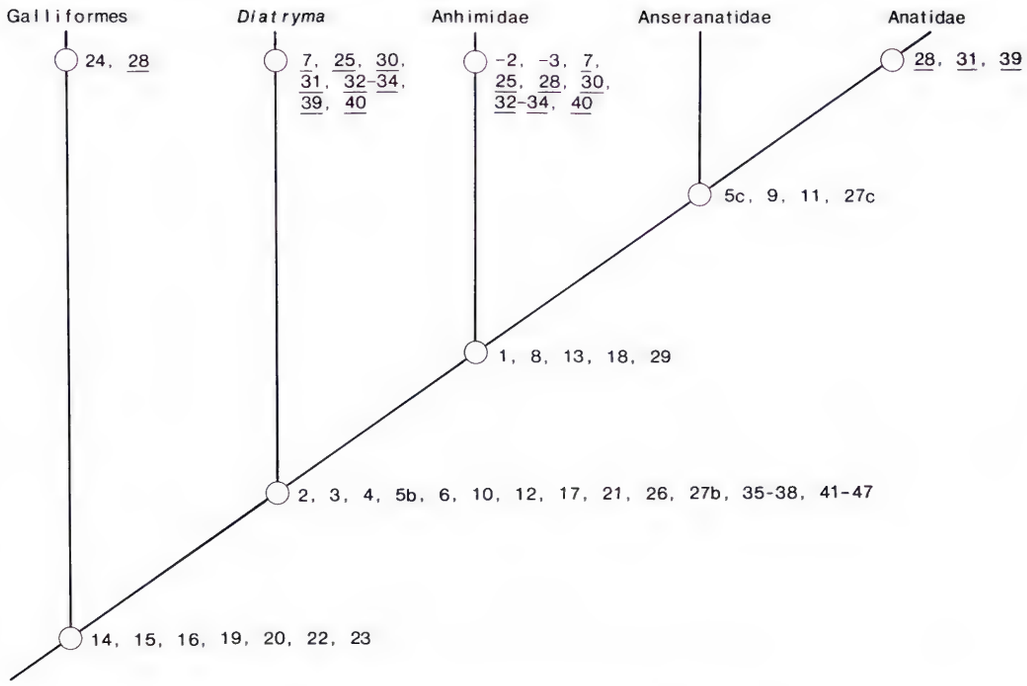

Figure 9. A phylogenetic hypothesis for the Galliformes, Anseriformes, and *Diatryma*. Numbers at internodes and branch ends correspond to postulated synapomorphies (coded b or c), character reversals (minus sign) and parallelisms (underlined) as discussed in the text and listed in Table 2.

heavy toes of *Diatryma* may imply graviportal posture and locomotion, which have been inferred for other large flightless herbivores (Storer, 1960; Cracraft, 1976). The intramembral proportions of the anterior toes are bustard-like, but the retention of a functional hallux distinguishes *Diatryma* from more cursorially adapted groundbirds, including bustards, in which the hind toe has been lost. It is postulated (Andors, 1988) that *Diatryma* seldom ran but, instead, moved typically at a slow pace, in the manner of a bustard. Its running ability was probably comparable to that of the extinct moa *Pachyornis* Lydekker 1891 (treated by Alexander, 1983b, 1985), which converged on *Diatryma* in pelvic and hindlimb proportions and in overall size.

PALEOBIOGEOGRAPHY

The presence of flightless diatrymids on both sides of the present-day North Atlantic is *prima facie* evidence that Europe and North America were once connected by dry land (Cracraft, 1973; Andors, 1988). Other Wasatchian/Ypresian birds, including the Lithornithidae (Houde, 1986), have similar disjunct distributions, as do some contemporaneous lower vertebrates (West et al., 1977; West and Dawson, 1978; Estes and Hutchison, 1980) and numerous mammals (McKenna, 1975, 1982; Godinot, 1982). McKenna (1975, 1982) has shown that geological and geophysical data are in basic accord with biologic evidence for the former existence of a land connection spanning the northern end of the Atlantic Ocean during part of the Early Eocene (see also Savage and Russell, 1983; Ziegler, 1988).

Either of two dispersal routes could have been used by *Diatryma* (Fig. 4), one corresponding to the Faeroe–Iceland–Greenland Ridge (the Thulean Route) and the other, which terminated in a Fennoscandian cul-de-sac, corresponding to the predrift juxtaposition of the Barents Shelf, Svalbard, Greenland, Ellesmere Island, and the Canadian mainland (the De Geer Route). From available evidence, it would appear that the fate of *Diatryma* was tied to that of a transient Thulean corridor, which permitted two-way dispersal for a brief period during the early Early Eocene before it was sundered by subsidence of the Iceland–Faeroe Ridge. After this overland connection was disrupted, North American populations may have been extirpated by regional elimination of backswamp plant communities associated with secular cooling and drainage reversal brought about by the Laramide orogeny (West and Dawson, 1978; Bown, 1980; Wing, 1980). In Europe, diatrymids lingered on somewhat longer, until the end of the Middle Eocene, when their lake-margin refugia were finally eliminated by continued climatic deterioration (Russell, 1975; Savage and Russell, 1983:130).

The sister-group of *Diatryma,* the Anseriformes, may have northern affinities, as may the sister-group of *Diatryma* + Anseriformes, the Galliformes. The oldest known screamer (undescribed), the oldest known duck (*Presbyornis* Wetmore 1926), and the oldest known galliform (*Gallinuloides* Eastman 1900) are all found in the Paleogene of the Northern Hemisphere. If *Diatryma* has been allied correctly with anseriforms and galliforms, then its zoogeographic affinities may lie with Laurasia and, perhaps, Euramerica. A Euramerican origin of the Gastornithiformes is at least consistent with known fossils, and it has the advantage of not invoking waif dispersal from Gondwanaland across persistent marine barriers (see Simpson, 1980: 251; Rage, 1981).

SUMMARY

The principal conclusions of this paper are the following.

1. The Diatrymidae, giant flightless groundbirds from the lower Tertiary of Holarctica, have an extensive fossil record in North

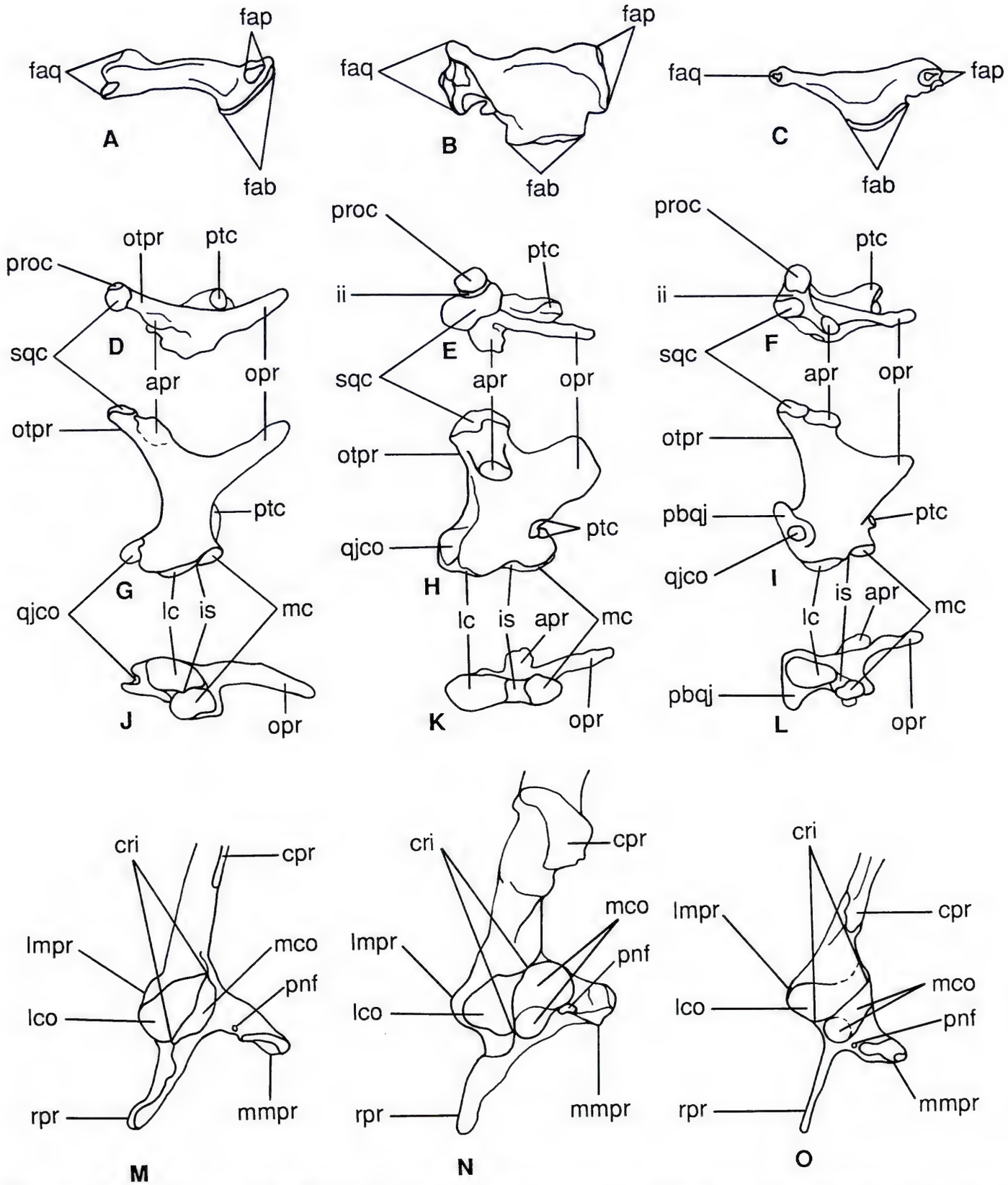

Figure 10. Right pterygoid (**A–C**), right quadrate (**D–L**), and left articular (**M–O**) of (left column) a galliform [*Meleagris gallopavo*, Phasianidae (AMNH Orn. 5091)], (center column) a gastornithiform [*Diatryma gigantea*, Diatrymidae (AMNH 6169)], and (right column) an anseriform [*Chauna torquata*, Anhimidae (AMNH Orn. 1773)] showing some features used in an analysis of the phylogenetic affinities of *Diatryma* (Table 2). Homologous bones have been drawn at the same absolute size in order to facilitate comparison. A, O, 1.7×; B, 0.6×; C, 2.4×; D, F, G, I, J, L. 1.8×; E, H, K, N, 0.4×; M, 1.9×. **A–C,** ventral; **D–F,** proximal (dorsal); **G–I,** anterolateral; **J–L,** distal (ventral); **M–O,** dorsal views.

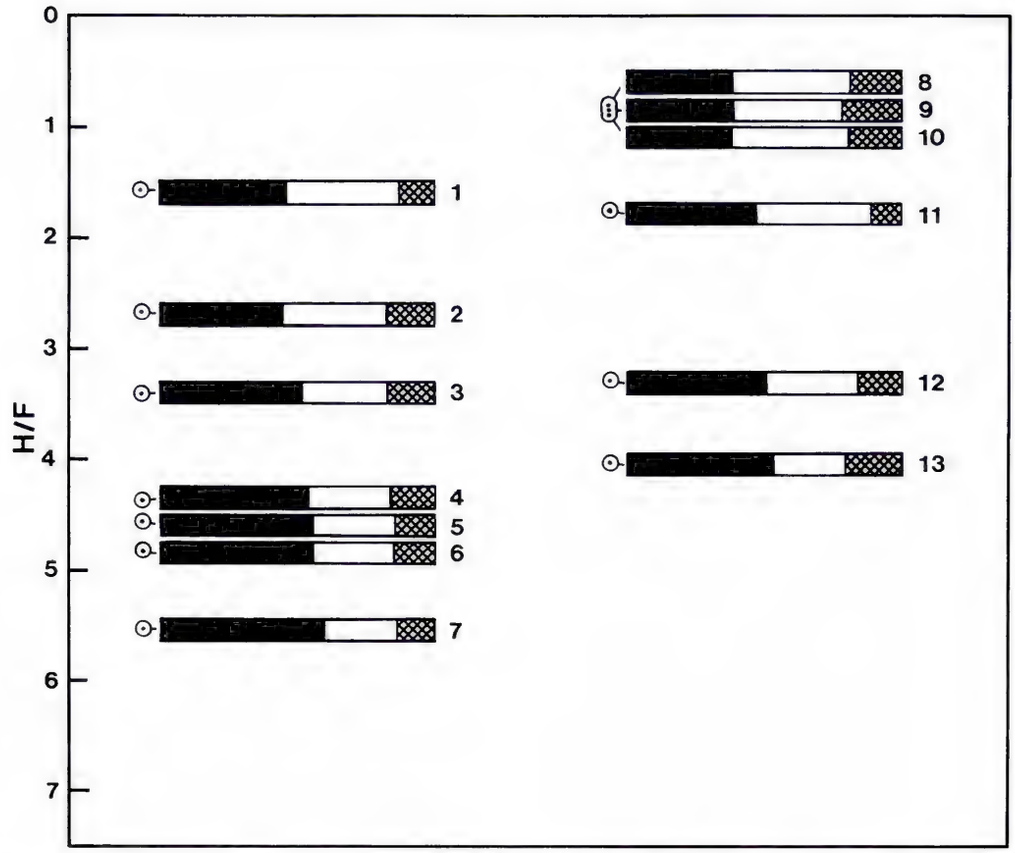

Figure 11. Patterns of forelimb reduction in selected clades of dinosaurs and birds. For each numbered taxon, the principal segments of the forelimb are represented schematically by shaded rectangles, as follows: black, humerus; white, ulna; cross-hatched, longest metacarpal (dinosaurs) or carpometacarpus (birds). All forelimbs are drawn to the same unit length and plotted as a function of hindlimb (H) : forelimb (F) ratio to facilitate comparison of intramembral proportions in related taxa with forelimbs of different relative size. H:F ratio correlates positively with body size. Source: Andors (1988). Pseudosuchia: **1,** *Ornithosuchus longidens* (Huxley 1877). Theropoda: **2,** *Allosaurus fragilis* Marsh 1877; **3,** *Daspletosaurus torosus* Russell 1970; **4,** *Albertosaurus libratus* (Lambe 1914); **5,** *Daspletosaurus* sp.; **6,** *Albertosaurus sarcophagus* Osborn 1905; **7,** *Tarbosaurus bataar* (Maleev 1955a). Anseriformes: **8,** *Anhima cornuta* (Linnaeus 1766); **9,** *Cereopsis novaehollandiae* Latham 1801; **10,** *Chauna chavaria* Linnaeus 1766; **11,** *Cnemiornis calcitrans* Owen 1866*; **12,** *Thambetochen chauliodous* Olson and Wetmore 1976*. Gastornithiformes: **13,** *Diatryma gigantea**. *, flightless.

America and Europe. The known corpus of Nearctic diatrymid material has recently been multiplied five-fold (Andors, 1988). Geographic range extensions documented in the latter study include occurrences of diatrymids in Colorado (Uinta Basin, Huerfano Park) and Wyoming (Green River Basin, Washakie Basin).

2. The temporal range of the Diatrymidae is less extensive in North America (Early Eocene) than in Europe (Early Eocene–Middle Eocene). The co-occurrence of *Diatryma*, the only diatrymid genus, in Wasatchian and Ypresian deposits can be interpreted as a first-appearance datum that marks the establishment of a transient terrestrial corridor between North America and Europe during the Early Eocene.

3. Depositional environments and associated floras and faunas indicate that diatrymids were inhabitants of coastal lowlands and alluvial floodplains. Specialization of *Diatryma* for life in humid, well-vegetated landscapes made it vulnerable to extinction when the period of relative tropicality that characterized the early Tertiary came to a close.

4. A redescription of the best-known diatrymid, *Diatryma gigantea* (Andors, 1988), provides the first reasonably complete picture of this landmark of fossil ornithology (Matthew and Granger, 1917). The ulna, carpometacarpus, and first metatarsal of that species were reported for the first time. Adult *D. gigantea* had a huge beak, weighed approximately 175 kg, and attained a height of about 2 m. The midpoint of growth in height was

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Abbreviations: **apr,** process for musculus adductor mandibulae externus profundus and associated aponeuroses; **cpr,** coronoid process; **cri,** crista intercotylaris; **fab,** facies articularis basipterygoidea; **fap,** facies articularis palatina; **faq,** facies articularis quadratica; **ii,** intercondylar incisure; **is,** intercondylar sulcus; **lc,** lateral condyle; **lco,** lateral cotyla; **lmpr,** lateral mandibular process; **mc,** medial condyle; **mco,** medial cotyla; **mmpr,** medial mandibular process; **opr,** orbital process; **otpr,** otic process; **pbqj,** posterior buttress for quadratojugal; **pnf,** pneumatic foramen; **proc,** proötic condyle; **ptc,** pterygoid condyle; **qjco,** quadratojugal cotyla; **rpr,** retroarticular process; **sqc,** squamosal condyle.

reached at an age of roughly 2–3 months. The beak in a half-grown bird was relatively shorter than in the adult.

5. Two European (*Diatryma sarasini, D. geiselensis*) and two predominantly North American (*D. gigantea, D. regens*) species of *Diatryma* are tentatively recognized. *Diatryma gigantea* may have ranged across a North Atlantic land bridge into Europe (Berg, 1965). *Diatryma* (?) *cotei* Gaillard is removed from the Diatrymidae and placed with Aves incertae sedis.

6. Pelvic limb features verify the relationship between *Diatryma* and *Gastornis* proposed by Cope (1876) and justify retaining these genera in separate families (Diatrymidae, Gastornithidae) within a single order (Gastornithiformes). Inclusion of *Zhongyuanus* in the Gastornithidae (Hou, 1980) must be regarded as provisional. As presently constituted, the Diatrymidae are Euramerican and the Gastornithidae are Eurasian in distribution.

7. Screamers (Anhimidae) are the sister-group of the waterfowl (Anseranatidae + Anatidae), and the Gastornithiformes are the sister-group of the Anseriformes (Anhimidae + Anseranatidae + Anatidae). The Galliformes may be the sister-group of the Gastornithiformes + Anseriformes.

8. The skull of *Diatryma* was prokinetic and apparently primarily adapted for herbivory. The diatrymid feeding mechanism is paralleled in part by Recent avian folivores (including the largest extant parrots and rails), which, not coincidentally, have lost or reduced their capacity to fly and have undergone correlated increase in body size. *Diatryma* was definitely not a "terror crane" (Kurtén, 1972), having possessed neither predatory adaptations nor features indicative of a relationship to cranes. Far from having posed a threat to animals high in the Eocene food chain, *Diatryma* appears to have occupied a lower trophic level than hitherto believed and to have assumed the role of a primary consumer.

9. *Diatryma* was ponderous and flightless, with a wing length (31 cm) comparable to that of a flying bird weighing a few kilograms or less. It is concluded that the diatrymid wing underwent reduction in a relative sense while body size increased. Transformation series of dinosaurian and avian forelimbs indicate that forelimb reduction in obligate bipeds, including diatrymids, tends to be concentrated distally.

10. The proportionately long femur, short tarsometatarsus, functional hallux, and bustard-like anterior toes of *Diatryma* are indications that the characteristic gait of this ground-dwelling bird was pedestrian, not cursorial.

11. The disjunct distribution of *Diatryma* on both sides of the present-day North Atlantic is paralleled by that of other Early Eocene vertebrates (mammals, lower vertebrates, other birds), which together indicate the presence of a terrestrial corridor between North America and Europe about 50 Ma.

12. The Gastornithiformes and the related Anseriformes and Galliformes may have originated in the Northern Hemisphere.

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A NEW FAMILY OF PRIMITIVE LANDBIRDS FROM THE LOWER EOCENE GREEN RIVER FORMATION OF WYOMING

Storrs L. Olson

ABSTRACT. A new family, Foratidae, is erected for *Foro panarium* new genus, new species, based on a nearly complete, associated skeleton from the Lower Eocene Green River Formation of Wyoming. The apparent lack of any of the locomotory or feeding specializations by which many modern families and orders of birds may be recognized makes assignment of this bird difficult. The skull and mandible are most similar to those in the Opisthocomidae, but the postcranial skeleton is very different, although some elements show similarity to the Musophagidae. The elongated hindlimb elements of *Foro*, especially the tarsometatarsus, suggest a more terrestrial mode of life than modern species of Musophagidae or Opisthocomidae, perhaps not unlike some of the terrestrial Cuculidae. Birds similar to the very generalized Foratidae could have given rise to the arboreal Opisthocomidae on one hand and to the terrestrial Cariamae on the other, and perhaps even to some of the diurnal raptors.

Key words: Eocene, Aves, Green River Formation, Foratidae, landbirds.

INTRODUCTION

Our knowledge of the Early Eocene avifauna of North America is increasing rapidly through study of excellent fossil material in freshwater limestone nodules from the Bighorn Basin of Wyoming (Houde, 1988; Houde and Olson, 1989) and from lacustrine shales and sandstones of the Green River Formation (e.g., Olson, 1977, 1987). The subject of the present paper (Fig. 1) is one of the best-preserved specimens recovered so far from the latter, a bird apparently otherwise unknown among the rather extensive Early Eocene collections now available and for which no other material has yet been recognized.

MATERIALS AND METHODS

The fossil was compared with a synoptic series of skeletons containing most of the modern families of non-passerine birds. After most of these were eliminated, the following specimens were used for more detailed comparisons and the descriptions. All catalogue numbers are in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). Musophagidae: *Crinifer africanus zonurus* Rüppell 1835, 430522; *Corythaixoides concolor* (Smith 1833), 558534; *Musophaga violacea rossae* Gould 1852, 558255; *Corythaeola cristata* (Vieillot 1816), 291079. Cuculidae: *Coua ruficeps* Gray 1846, 432195; *Cuculus canorus* Linnaeus 1758, 603559; *Crotophaga major* Gmelin 1788, 500421; *Geococcyx californianus* (Lesson 1829), 499279; *Centropus goliath* Bonaparte 1850, 557169. Opisthocomidae: *Opisthocomus hoazin* (Müller 1776), 344065. Megapodiidae: *Megapodius freycinet* Gaimard 1823, 560650. Cracidae: *Ortalis vetula* (Wagler 1830), 288729. Falconidae: *Milvago chimachima* (Vieillot 1816), 343844, Accipitridae: *Accipiter gentilis* (Linnaeus 1758), 610350. Cariamidae: *Cariama cristata* (Linnaeus 1766), 19941; *Chunga burmeisteri* (Hartlaub 1860), 431487. Anatomical terminology is modified from Howard (1929).

SYSTEMATICS

Class Aves Linnaeus 1758

Subclass Ornithurae Haeckel 1866

CHARACTERS. The tail in the fossil consists of only 6 free caudal vertebrae and a well-developed pygostyle, unlike the reptilian tail of *Archaeopteryx* von Meyer 1861 (Sauriurae).

Superorder Neognathae Pycraft 1900

CHARACTERS. The specimen is edentulous and cannot be included in any superorder containing *Hesperornis* Marsh 1872, *Ichthyornis* Marsh 1872, or their respective allies (the so-called Odontornithes, Odontognathae, or Odontoholcae of various authors). Although the palate itself cannot be discerned, the fossil clearly cannot be included in the superorder Palaeognathae either. The skull in paleognathous birds is adapted for what Zusi (1984:5) has termed "central rhynchokinesis," in which there is a "single bending zone of the dorsal bar . . . located approximately midway between the symphysis and the lateral bars and the nares extend back to the cranial attachments of the lateral bars." Concomitant with this type of rhynchokinesis is the lack of fusion of the lateral bar of the nasal with the ventral bar of the premaxilla. The bill in the fossil, however, is short and stout, with rounded nostrils that do not extend far posteriad and a very heavy, complete, lateral nasal bar that is broadly fused to the ventral bar of the premaxilla (Fig. 2). This is, therefore, a holorhinal, prokinetic skull that by definition cannot have been paleognathous. The postcranial skeleton is not that of a flightless ratite, nor does it have any of the characteristic features of the Tinamidae or the Lithornithidae (Houde, 1988), the only known groups of volant paleognathous birds.

Figure 1. *Foro panarium* n. gen., n. sp., holotype (USNM 336261), nearly complete skeleton.

There is thus no reason to associate the fossil with any of the Palaeognathae, and it is typical of the modern radiation of neognathous birds.

REMARKS. For the most part, the systematic position of the fossil may be further refined mainly by the absence of derived characters. The short, rather generalized holorhinal bill is not obviously adapted for probing, spearing, filter-feeding, grasping fish, tearing meat, gaping, or catching flying insects. The wings are rather short and lack any adaptations for gliding or soaring, rapid aerial locomotion or hovering, or propulsion under water. The hindlimb and pelvis exhibit no adaptations for swimming or diving, or for raptorial grasping, the legs being long and gracile. In addition, the coracoid has a broad, well-developed procoracoid process; there is no ectepicondylar spur on the humerus, the pectoral crest of which is broad and rounded, not pointed and triangular; the carpometacarpus is short, the intermetacarpal process is lacking, and the minor metacarpal is broad and bowed and does not extend distad beyond the major metacarpal; the foot is anisodactyl, with no hint of even incipient zygodactyly.

With regard to the major informal groupings of birds used by Olson (1985), this combination of characters eliminates from consideration all members of the waterbird assemblage except the Cariamidae, all of the higher landbirds, and the Cuculidae, Falconiformes, Turnicidae, Columbiformes, and Psittaciformes among the basal landbird assemblage.

Among the groups that remain, the Galliformes differ from the fossil in having a much larger, blade-like retroarticular process of the mandible; longer and narrower scapula; much longer and narrower coracoid with no procoracoid process; the sternum with large, fused spina externa and spina interna, the body much more elongated, especially on the midline, with the lateral notches situated much farther anteriorly; minor metacarpal not broad and flat; pectoral crest of the humerus much reduced and the head of the humerus more bulbous. The modern Cariamidae differ from the fossil in having a simple, block-like hypotarsus; a more elongate sternum, with only 2 notches; the acromion of the scapula much better developed; narrower procoracoid process; a smaller pectoral crest of the humerus; straighter shaft of the ulna; much weaker ectethmoid; and much more elongated bill.

This leaves only the Opisthocomidae and Musophagidae, with which the fossil indeed shares certain similarities. Both of these families have been included with the Cuculidae in or near an order Cuculiformes by some authors (e.g., Sibley and Ahlquist, 1973; de Queiroz and Good, 1988), although sometimes on indefensible evidence (Brush, 1979). The Opisthocomidae, Musophagidae, and Cuculidae probably do not constitute a monophyletic group in any sense of the word. If they are among the most primitive of the neognathous birds, as I have suggested (Olson, 1985), they may lack derived characters by which they can be united either as a group or with other orders or families of Neognathae. Nevertheless, if the fossil must be placed in any currently recognized ordinal taxon, it would by default have to be the Cuculiformes.

Order Cuculiformes Wagler 1830

CHARACTERS. By the retention of a very broad, prominent pectineal process of the pelvis, the fossil resembles most members of the Cuculiformes. In shape, this process in the fossil is most similar to that in the Musophagidae, whereas in the Cuculidae it is more slender and pointed, when present, as it has evidently been lost in some of the Cuculidae as well as in the Opisthocomidae. Elsewhere among the Neognathae, the pectineal process apparently occurs only in numerous genera of the galliform family Phasianidae, from which the fossil differs in the characters previously mentioned. The pectineal process is also present in all members of the Palaeognathae, and it is probably primitive within Aves.

Family Foratidae new family

TYPE GENUS. *Foro* new genus, the only included genus.

DIAGNOSIS. Holorhinal, anisodactyl Neognathae having open nostrils without secondary ossification; broad procoracoid process; accipitrid-like humerus with pectoral crest long, broad, curved, and proximally situated; short, broad, bowed minor metacarpal; and broad, prominent pectineal process of the pelvis. The overall shape of the cranium and bill; the strong, deep mandible; and the short, hook-like retroarticular process are similar to those of the Opisthocomidae. The vertebral number and overall shape of the coracoid, pelvis, carpometacarpus, and distal end of the tarsometatarsus are similar to the Musophagidae. The following characters distinguish the family from the Opisthocomidae: fewer presacral vertebrae; notarium absent; 5 rather than 6 caudal vertebrae; and sternum and furcula not bizarrely modified to accommodate the enlarged crop. From the Musophagidae, the Foratidae differ in not having the rostrum elevated and inflated; the spina externa of the sternum is not large and blade-like; the procoracoid process is not fused to the head of the coracoid to form a complete bony ring; the clavicles are united, rather than being unfused and articulating with each other by a synovial joint; and the scapular tuberosity and coracoidal facet are not nearly as well developed. In addition to lacking any hint of zygodactyly, the Foratidae differ from the Cuculidae in the much less elongated rostrum; the ectethmoid is not large and inflated; and the hypotarsus is longer with apparently only one, rather than two, enclosed bony canals. The Musophagidae and most Cuculidae have large, distinct papillae on the ulna for the attachment of secondary feathers, which is probably a condition that has been derived independently in several groups of birds, but which is lacking in the fossil and in the Opisthocomidae.

Foro new genus

TYPE SPECIES. *Foro panarium* new species.

DIAGNOSIS. As for family.

REMARKS. The hindlimb elements, especially the tarsometatarsus, are quite slender and elongated, being similar in absolute size to those of a roadrunner (*Geococcyx* Wagler 1831: Cuculidae). This suggests that the bird was to some extent terrestrial, unlike the Opisthocomidae and Musophagidae, which are exclusively arboreal. Lengthening of the tarsometatarsus as an apparent terrestrial adaptation may occur within an otherwise arboreal family (e.g., Cuculidae, Columbidae) or even within a genus [e.g., *Athene* (*Speotyto auct.*) *cunicularia* (Molina 1782): Strigidae].

ETYMOLOGY. See etymology of species.

Foro panarium new species

Figures 1–7

HOLOTYPE. Essentially complete associated skeleton, vertebrate paleontological collections of the National Museum of Natural History, Smithsonian Institution, USNM 336261; collected in 1982.

DIAGNOSIS. As for family.

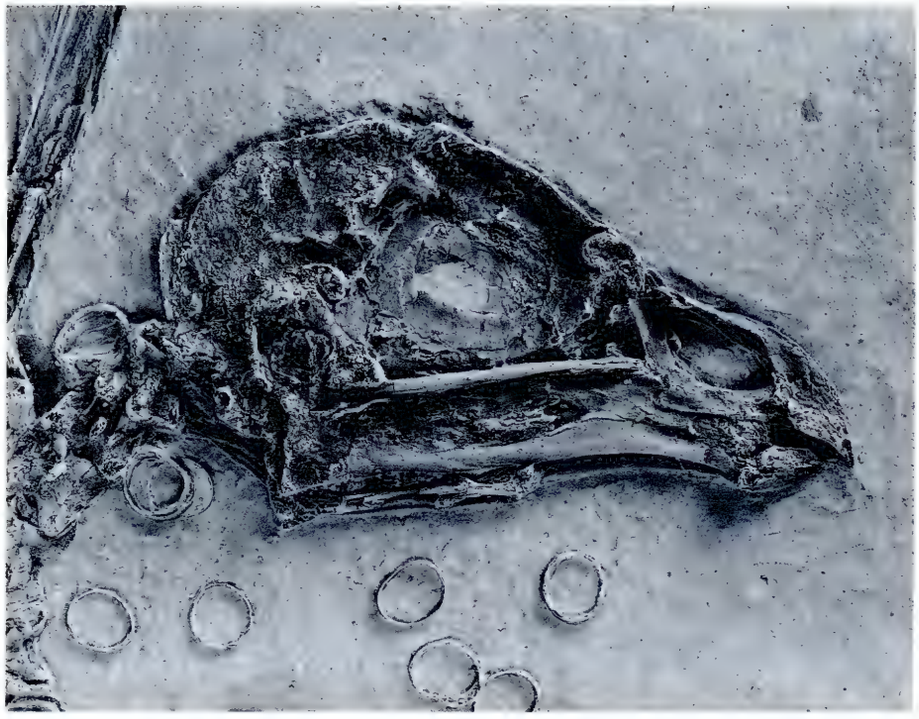

Figure 2. Detail of skull of holotype of *Foro panarium* n. gen., n. sp. (USNM 336261). 1.5×.

TYPE LOCALITY. "Thompson Quarry," northwest of Kemmerer, Lincoln County, Wyoming: NW¼, SW¼, sec. 22, T22N, R117W (Kemmerer 15-minute quadrangle); 41°44′N, 110°31′W. This is the site indicated in Feldmann et al. (1981:789, fig. 1) and is among the F-2 localities of Grande (1984).

HORIZON. Fossil Butte Member of the Green River Formation, upper Lower Eocene (Wasatchian Land Mammal age).

ETYMOLOGY. Dedicated to Pierce Brodkorb, of whose name this is a direct latinization: L. *foro, foratus,* pierce, bore (cf. perforate, foramen); *panarium,* breadbasket (*ex* Brodkorb, from German *Brot* or *Brod,* bread, and *Korb,* basket). By analogy with *Vireo,* also a first-person singular verb, the generic name may be considered masculine in gender. The specific name is a noun in apposition. I would have preferred these names in reverse order but unfortunately *Panarium* is preoccupied by a genus of Protista (Haeckel, 1882).

MEASUREMENTS (mm) OF HOLOTYPE. Skull: total length, 60.1; length of rostrum from nasofrontal hinge, 22.9; length of premaxillary symphysis, 9.9; length of nostril, 12.1; length of mandible, 45.9. Sternum: approximate length, 43; width at posteriormost costal facet, 24.5. Coracoid: length to internal sternal angle, 25.3; width of sternal end, 14.1. Scapula: length, 43.9; width of articular end, 8.8; least width of neck, 3.3. Humerus: length, 52.5; distal width, 9.0. Ulna: length, 50.0. Radius: length, 44.5. Carpometacarpus: length, 26.7; proximal depth, 8.8. Alular digit: length of phalanx 1, 8.6; length of phalanx 2, 2.0. Major digit: length of phalanx 1, 10.8; length of phalanx 2, 7.7. Pelvis: length along midline, 43.1; length to posteriormost point of ischium, 58.9; width across antitrochanters, 29.2. Femur: length, 54.1. Tibiotarsus: length from inner cnemial crest, 88.4; depth through external condyle, 7.5. Tarsometatarsus: length, 61.3; distal width, ca. 9.3. Metatarsal I: length, 5.4. Lengths of phalanges of pes: I1, 9.2; I2, 4.8; II1, 12.4; II2, 10.9; II3, 7.3; III1, 13.9; III2, 12.1; III3, 11.6; III4, 8.3; IV1, 8.9; IV2, 7.0; IV3, 6.3; IV4, 7.3; IV5, 6.6. Tracheal rings: greatest diameter (average of 5), 5.5. Pygostyle: length, 15.4.

PRESERVATION OF THE SPECIMEN. The fossil (Fig. 1) is brown in color and it is preserved in a block of cream-colored shale containing scales and coprolites of fish. Most of the bones are present in their entirety (not split longitudinally) with the long bones being reasonably three dimensional, though with the shafts variously crushed. The slab had been broken into at least four pieces, all the cracks having been neatly repaired with little damage to the specimen except for a large crack running in front of the pectoral apparatus and the left wing. Damage in this area has destroyed the left alular metacarpal and phalanges, obliterated all details of the left carpometacarpus, and probably removed at least one vertebra and a number of tracheal rings. As preserved and prepared, the bird is seen essentially in dorsal view, with the head thrown back and the vertebral column variously disarticulated.

The skull, complete with sclerotic ring and mandible, is seen in right lateral view, with 7 cervical vertebrae in articulation. The vertebral column continues as a loop of 6 vertebrae (one represented by a zygapophysis only) in front of the pectoral apparatus, and, as mentioned, at least one vertebra has probably been completely destroyed in this area. Three thoracic vertebrae lie directly on top of the sternum, which is seen in dorsal view, and the last two lie in articulation to the right of the sternum. The pelvis is disassociated from the body and from the femora and lies in dorsal and right lateral view, partially obscuring the proximal end of the right tibiotarsus. The left ischium is bent completely under the pelvis and protrudes with its medial side uppermost in the space between the posterior processes of the ilia. The tail is removed a short distance from the pelvis and has 6 free caudals (probably all that were present) in articulation

Figure 3. Detail of pectoral apparatus, in dorsal view, of *Foro panarium* n. gen., n. sp., holotype (USNM 336261). Arrow indicates the medial sternal notch; the remains of the lateral sternal notch are mostly obscured by the displaced portion of the posterior lateral process. The two portions of the broken clavicle are indicated by F. 1.5×.

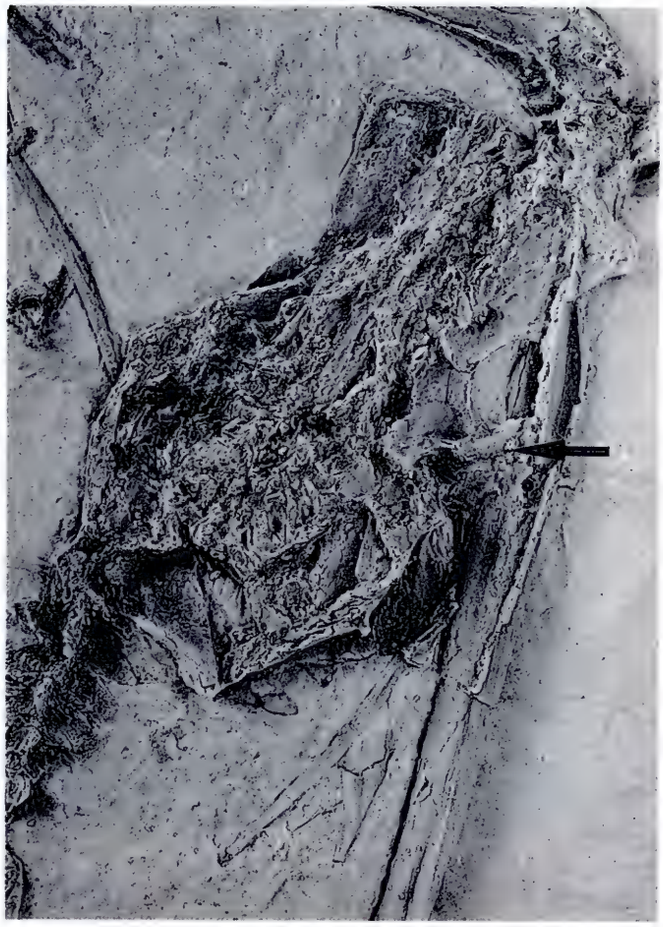

Figure 4. Detail of pelvis of holotype of *Foro panarium* n. gen., n. sp. (USNM 336261). Arrow indicates the large pectineal process. 1.5×.

with the pygostyle, which is turned so as to be seen in left lateral view.

The furcula is almost completely exposed, with the left ramus broken and lying at right angles to the remainder. Both ends of the left coracoid are obscured by the sternum and left clavicle, but the shaft and procoracoid process are visible. The right coracoid is overlain by the right scapula, but most of its outline except the procoracoid process may be discerned. Both scapulae are nearly fully exposed in dorsal view. The entire left margin of the sternum, except the sternocoracoidal process, is obscured by the left scapula and ribs.

The left wing is seen in dorsal view, with the carpometacarpus and alular digit missing or obliterated, but major and minor digits remain in close articulation. The right wing is seen in ventral view, with the phalanges being completely disarticulated, and that of the minor digit apparently missing. The distal phalanx closest to the alular metacarpal is identical in size and shape to phalanx 2 of the major digit of the left wing. Therefore, the phalanx abutting the right carpometacarpus at right angles, which is longer than the other, is taken to be the alular phalanx, or rather I should say the proximal alular phalanx, because at its distal end is a small bone that I interpret as a second phalanx, or wing claw.

Both femora and tibiotarsi are seen in lateral view, with much of the shaft of the left tibiotarsus missing. The right tarsometatarsus is seen in posterior view, with the toes in ventral view; the left tarsometatarsus and toes are essentially in left lateral view.

DESCRIPTION AND COMPARISONS. The overall similarity of the skull and mandible (Fig. 2) is decidedly closer to that in the Opisthocomidae than to either the Musophagidae or Cuculidae. The cranium in lateral view is rather elongate and ovoid, and the bill fairly deep and quite short, much less than half the total length of the skull. The rostrum is not elevated and inflated, as in all the Musophagidae, nor elongated as in the Cuculidae.

The nostril is open and unossified, the ventral nasal bar being quite distinct and broad. This is in contrast to the Musophagidae, Opisthocomidae, and most Cuculidae, in which the nostril is heavily ossified and the opening greatly reduced in size. Even in those members of the Cuculidae in which the nostril is relatively open, and the ventral nasal bar distinct, the nasal septum is still heavily ossified and the nares are not obviously perforate, as they are in the fossil.

The sclerotic ring is in place and the number and pattern of

Figure 5. Humeri, radii, and ulnae of the holotype of *Foro panarium* n. gen., n. sp. (USNM 336261). **A.** Left wing in anconal view. **B.** Right wing in palmar view. 1.5×.

overlap of the ossicles can be discerned reasonably well. Variation in the sclerotic ring of the Galliformes and Cuculiformes has been analyzed and discussed by de Queiroz and Good (1988). The number of ossicles in the fossil appears to be 13. The anterior portion of the ring has suffered some damage and it is the more difficult to interpret, so that it is possible that the number may be 14. The pattern of overlap, following the numbering convention adopted by de Queiroz and Good (1988), is 1+, 4−, 7+, 10−. This number and pattern is essentially identical to that illustrated by de Queiroz and Good (1988:fig. 1f) for the Musophagidae except that the 10th rather than the 9th ossicle is overlapped on both sides by adjacent ossicles. The typical number of ossicles in the Musophagidae is 13 (varying from 11 to 14), whereas in the Cuculidae and Opisthocomidae it is usually 12 (varying from 11 to 14 and 11 to 13, respectively) and in the Galliformes 14 or 15 (sometimes 13). Although the modal number of ossicles may be characteristic for a given higher-level taxon, variation within species and families would appear to render this character largely inconclusive for taxonomic purposes when dealing with a single specimen.

Very little detail can be made out concerning the rest of the skull, except that there is a small, thin ectethmoid plate present, similar to that in the Musophagidae and Opisthocomidae and unlike the larger and much more inflated ectethmoid in the Cuculidae. Because of damage, the presence of a prefrontal (lacrimal) bone cannot be ascertained, though if present it would have to be quite small.

The mandible is deep and straight, with a robust, pointed symphysis, in which respects it bears strong resemblance to that in the Opisthocomidae. There is no marked ventral depression of the dentary portion as in the Musophagidae. The extent of what appears to be an open mandibular foramen is difficult to determine because of underlying bone that has been crushed into it, perhaps from the opposite ramus. There is a well-marked, short, upturned retroarticular process, very similar to that in the Opisthocomidae. This process is absent in the Musophagidae and Cuculidae.

Assuming that one vertebra was lost through damage, there are 19 presacral vertebrae, as in the Musophagidae. In the Cuculidae there are 18 and in the Opisthocomidae 21, of which 4 thoracics are fused into a notarium, a feature definitely lacking in the fossil.

The sternum (Fig. 3) is short and rather square in outline, with a short, peg-like spina externa; short, blunt sternocoracoidal processes; and four shallow, rounded notches on the posterior border, the lateral notches being deeper than the medial. This is quite unlike the Musophagidae, in which the spina externa is large and blade-like and the four notches are much deeper and more V-shaped. The sternum in the Cuculidae may vary from four rather deep notches to two very shallow ones. In the Opisthocomidae, some individuals may have four notches that are somewhat similar to those in *Foro,* whereas in others these are reduced to two broad, shallow notches. Deep notches, such as those in the Musophagidae are probably primitive. Re-

duction in size and number of sternal notches is a prevalent phenomenon that has occurred in disparate lineages of birds (e.g., Fregatidae and Steatornithidae; see Olson, 1977, 1987).

The overall similarity of the coracoid (Fig. 3) is closer to the Musophagidae, but the procoracoid process does not fuse with the head to produce a coalesced ring that excludes the clavicle from the triosseal canal, a derived character of the Musophagidae. Also, the scapular facet is deeper. The coracoid is unlike that in the Cuculidae, in which the shaft is longer and more slender, the sternal end narrower, and the head more pointed. It is also unlike that in the Opisthocomidae, in which the shaft is also slender, with a pneumatic sternal end that abuts the adjacent coracoid on the midline of the sternum.

The blade of the scapula (Fig. 3) is more expanded than in the Musophagidae or especially the Cuculidae and is thus more similar to that in the Opisthocomidae. The acromion is not as well developed as that in the Opisthocomidae or Musophagidae, being shorter and blunter, more as in the Cuculidae.

The furcula (Fig. 3) is broadly U-shaped with rather wide, flat shafts, no apparent hypocleideum or scapular tuberosity, and poorly developed coracoidal facets. This is totally unlike the Musophagidae, in which the clavicles are unfused and there is a large scapular tuberosity and prominent coracoidal facet. It is also unlike the unusual Y-shaped furcula of *Opisthocomus* Illiger 1811, which is fused to the pectoral girdle both anteriorly and posteriorly. The furcula in the Cuculidae is variable, but it usually has a hypocleideum and narrower shafts that are not spaced as far apart. The furcula of *Foro* seems to be very generalized, especially compared with either the Musophagidae or Opisthocomidae.

The pelvis (Fig. 4) of *Foro* lacks the laterally flared points of the anterior part of the ilium seen in the Cuculidae, and its overall resemblance is close to the Opisthocomidae and Musophagidae, except that the ischium is more pointed and posteriorly directed, and the pectineal process is lacking in the Opisthocomidae.

The pectoral crest of the humerus (Fig. 5) is long and broad, with a curved apex, unlike the short, ventrally rotated crest in the Cuculidae or the pointed and much more distally situated crest in the Musophagidae or Opisthocomidae. The shaft is short and relatively straight, being much less curved than in most of the Cuculidae. The entepicondylar area is not as strongly produced ventrally as in most Cuculidae, and the bicipital crest is more pronounced than in any of the Cuculiformes. The overall similarity of the humerus is actually closest to that in the Accipitridae, a group of uncertain ancestry but postulated to have had a possible origin in the "cuculiform" basal landbirds (Olson, 1985). The diurnal raptors have a much longer forearm and manus than in *Foro,* however, and there are no other striking similarities between the fossil and the diurnal raptors.

The ulna (and radius) is proportionately short (Fig. 5). The olecranon is squared and scarcely projects beyond the cotylae. The shaft is relatively straight, with no evidence of the exaggerated papillae for the secondaries that are characteristic of the Musophagidae and most Cuculidae, but not the Opisthocomidae. Contrary to what has frequently been written about *Archaeopteryx* to the effect that its secondaries must have been weakly attached because there are no papillae for them on the ulna, many modern birds lack prominent papillae for the secondaries, the attachment of which may even be indicated by depressions in the ulna rather than protrusions. The exaggerated secondary papillae in the Musophagidae and most Cuculidae, as well as in the Pici, are exceptional and probably represent a derived state.

Figure 6. Detail of right manus of holotype of *Foro panarium* n. gen., n. sp. (USNM 336261). Arrow indicates the presumed second phalanx of the alular digit. 1.5×.

The carpometacarpus (Fig. 6) is short, with a bowed minor metacarpal that is broad and flat proximally, as in most basal landbirds (Olson, 1985). The bowed condition is not as exaggerated as in most Cuculidae, in which there is a wider intermetacarpal space. The similarity is greater to the Musophagidae and Opisthocomidae. There appears to have been a second (ungual) phalanx on the alular digit (Fig. 6), as is the case in at least some adults of *Opisthocomus,* the young of which are renowned for their clawed fingers.

The shaft of the femur is relatively stouter and straighter than in the Musophagidae, Opisthocomidae, or Cuculidae, being somewhat more similar to the Accipitridae or Falconidae in this regard.

The tibiotarsus can be seen only in lateral view in the fossil. It is long and slender, with the outer cnemial crest much better developed than in the Musophagidae, Cuculidae, Opisthocomidae, or the diurnal raptors.

The tarsometatarsus (Fig. 7) is very long and slender, quite unlike that in the Opisthocomidae or Musophagidae. The hypotarsus is damaged on both sides of the specimen. It is relatively elongated, with a shallow medial groove and a very deep, more lateral groove that was probably enclosed or nearly so. Its similarity is thus closest to the Musophagidae and Opisthocomidae. It is decidedly unlike the short, block-like hypotarsus, with two enclosed canals, seen in the Cuculidae. The distal end of the tarsometatarsus shows no modification toward zygodactyly, and the overall configuration is very similar to that in the more primitive genera of Musophagidae such as *Crinifer* Jarocki 1821 or *Corythaixoides* Smith 1833.

In absolute size, the hallux is about equal to that in *Tauraco*

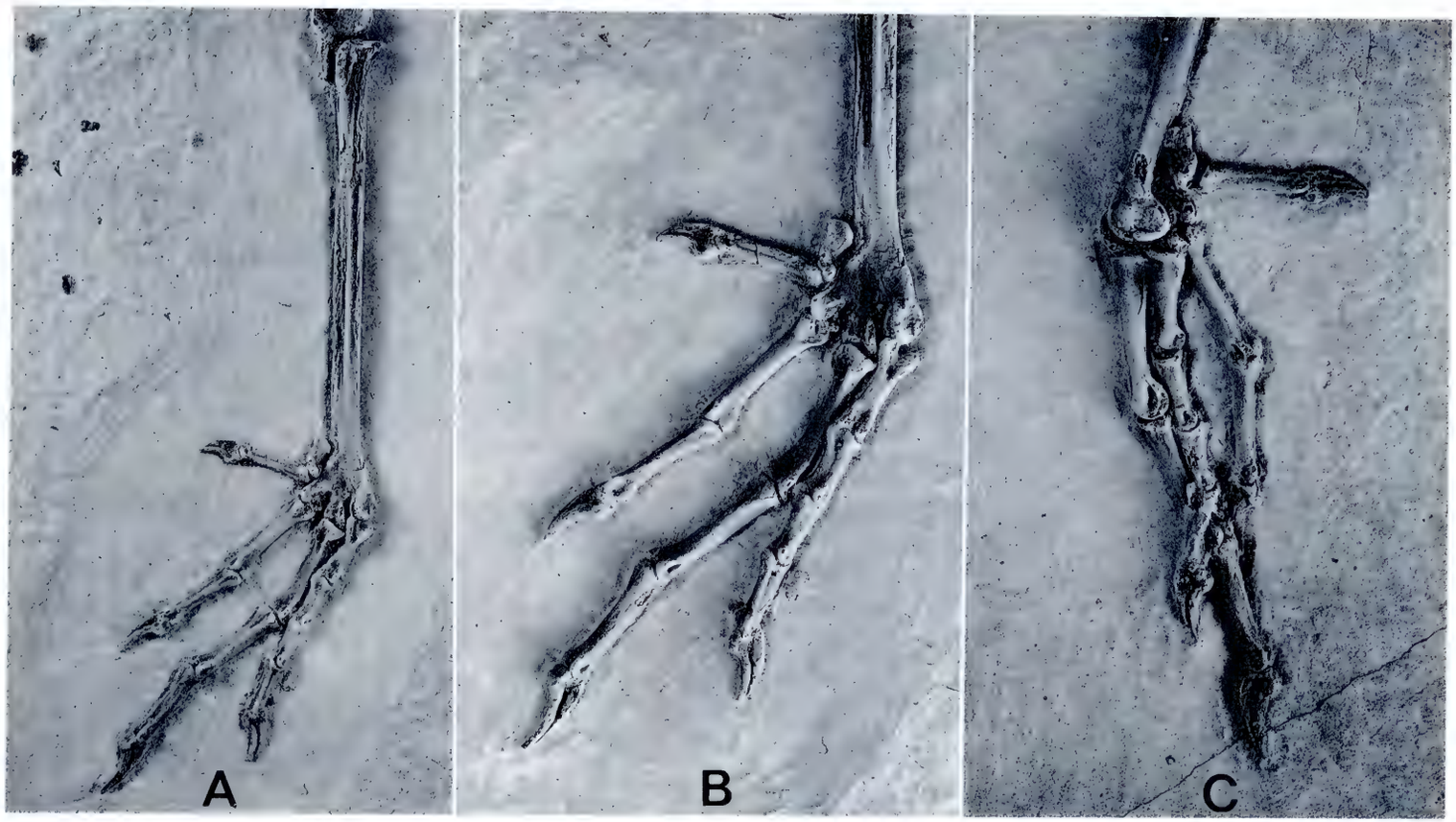

Figure 7. Feet of holotype of *Foro panarium* n. gen., n. sp. (USNM 336261). **A.** Right tarsometatarsus and toes (1×). **B.** Detail of right foot (1.5×). **C.** Detail of left foot (1.5×).

Kluk 1779, but shorter than in *Geococcyx*, whereas all the anterior toes are longer than in either of those genera. The claws are rather short and deep, unlike the longer more slender ones of *Geococcyx* but similar to *Tauraco*, except not as curved.

DISCUSSION

The overall similarity of the skull and mandible of *Foro* to those of *Opisthocomus* are actually quite striking, even to size and proportions. The chief observable difference is the posterior ossification of the nostril of *Opisthocomus*, which has reduced the size of the narial opening. This is, however, a pattern that is apparently repeated in completely different lineages, in which Early Eocene members have more open nostrils than their modern descendents [e.g., Steatornithidae (*Prefica* Olson 1987 vs. *Steatornis* Humboldt 1817; see Olson, 1987) and Fregatidae (*Limnofregata* Olson 1977 vs. *Fregata* Lacépède 1799; see Olson, 1977)].

The short, upcurved retroarticular process may be a derived character uniting *Foro* and *Opisthocomus*, one that perhaps foreshadows the longer, blade-like hook of the Galliformes. For this to be primitive it would have to have been lost in the Musophagidae and the Cuculidae, either once or independently.

The Opisthocomidae may be among the most primitive of living birds (Olson, 1985), and they are well known for the presence of well-developed reptilian-like claws on the wings of the young (Beddard, 1889). The adults of at least some individuals of *Opisthocomus* retain a second phalanx on the alular digit (its consistent presence is difficult to assess because this small bone is easily lost in skeletal preparations), as does the holotype of *Foro panarium*. This phalanx may be variously present in different groups of modern birds (Fisher, 1940).

Opisthocomus is highly arboreal, with a peculiar diet (for a bird) that includes a preponderance of leaves (Beebe, 1911). Consequently, it has a greatly enlarged crop for which the pectoral girdle, especially the sternum and furcula, is extremely modified (Perrin, 1875; Gadow, 1891; Böker, 1929). For these reasons, and also because of modifications of the vertebral column, most notably the presence of a notarium, there is little similarity in the postcranial skeletons of *Foro* and *Opisthocomus*, other than in the general resemblance of the pelves (except for the pectineal process, which is absent in *Opisthocomus*) and carpometacarpi and in the absence of secondary papillae on the ulna.

Miller (1953) described an avian cranium from the Miocene of Colombia as an opisthocomid, *Hoazinoides magdalenae*. I cautioned that this might have come from a bird with postcranial adaptations very different from those of *Opisthocomus* (Olson, 1985). As shown by *Foro panarium*, with its hoatzin-like head, such caution was well justified.

It has been suggested that there may be a much closer relationship between the Opisthocomidae and the Cariamidae than had previously been suspected (Mourer-Chauviré, 1983; Olson, 1985). This conclusion arose in the similarity of some of the elements, particularly the humerus, of the fossil group Idiornithinae, to those in *Opisthocomus*. The Idiornithinae were included as a subfamily of the Cariamidae by Mourer-Chauviré (1983:139), although she remarked that they were "equally close to the genus *Opisthocomus*." The overall appearance of the tarsometatarsus of *Foro panarium* bears a strong resemblance to that of *Idiornis* Oberholser 1936 itself. In those elements that are known, the idiornithines differ from *Foro* and agree with the Cariamidae in the shape of the humerus and the size and position of the pectoral crest and also in the much straighter shaft of the ulna.

Nevertheless, because *Foro panarium* is such a generalized bird, it is not difficult to envision something similar as giving rise both to the Opisthocomidae and to the suborder Cariamae, which is now included in the Gruiformes. Furthermore, the humerus in *Foro* is sufficiently similar to that in the Accipitridae to suggest that their ancestry may also be traceable to a bird not unlike *Foro*. The mosaic of characters seen in *Foro* is not unexpected in so ancient a bird and, in the final analysis, may substantiate an origin of the modern neognath radiation among the basal landbirds.

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A RADIATION OF COLY-LIKE BIRDS FROM THE EOCENE OF NORTH AMERICA (AVES: SANDCOLEIFORMES NEW ORDER)

Peter Houde and Storrs L. Olson

ABSTRACT. A new order and family (Sandcoleiformes: Sandcoleidae) is erected for the Middle Eocene genera *Eobucco* Feduccia and Martin 1976, *Uintornis* Marsh 1872, and *Botauroides* Shufeldt 1915 of Wyoming and three new genera, *Sandcoleus*, *Anneavis*, and *Chascacocolius* from the Lower Eocene of Wyoming. Sandcoleiforms were coly-like (Coliidae) in appearance, but they exhibited very different bill specializations. They were not closely related to any extant orders; nevertheless, they were probably closer to colies than to any other birds currently known.

Key words: Eocene, Wyoming, calcareous nodules, Coliiformes, Primobucconidae.

INTRODUCTION

The diversity of known Early Eocene avian fossils from North America has dramatically increased since 1980 with the discovery of abundant vertebrate "microfossils" in calcareous nodules in the Willwood Formation of Wyoming (Houde, 1988). Fossils from this formation were generally known from mudstone and channel-sand deposits (Bown, 1980); thus, these nodules are significant as an overlooked and unexploited resource of fossils in an area that has been the subject of intensive paleontological surveying for more than a century. In addition, they preserve the association and three-dimensional integrity of even extremely fragile fossil skeletons. By contrast, traditional surface collecting and screen-washing techniques typically yield unassociated, fragmentary elements. Non-avian bones are usually much more abundant than avian remains in nodules. The nodule avifauna fills a substantial gap because the species represented are almost completely different from those of the stratigraphically contiguous mudstones. Furthermore, faunal associations are often similar from one nodule to another, suggesting a nonrandom mode of concentration or formation within a distinctive microenvironment.

We have collected and prepared large numbers of bird fossils from calcareous nodules in the Sand Coulee area of the Clarks Fork Basin of Wyoming (Fig. 1) continuously since 1981. Paleognathous carinates (Lithornithiformes Houde 1988) are the most abundant birds in the calcareous nodules and were the first avian group from them to be reported. The next most commonly represented group in the nodule avifauna is an unnamed order, described herein, that includes the genus *Eobucco* Feduccia and Martin 1976 and, probably, *Uintornis* Marsh 1872 and *Botauroides* Shufeldt 1915. *Eobucco*, *Uintornis*, and *Botauroides* were known only from holotypical tarsometatarsi from the Middle Eocene Bridger Formation, southwestern Wyoming. These genera were previously placed in the Eocene family Primobucconidae Feduccia and Martin 1976. By preparing some of the holotypes of the Primobucconidae for the first time [i.e., *Neanis schuchertii* (Shufeldt 1913), "*Neanis*" *kistneri* (Feduccia 1973), and "*Primobucco*" *olsoni* Feduccia and Martin 1976], we discovered that this family is polyphyletic (Houde and Olson, 1989). Some genera are obligate zygodactyls belonging to the suborder Galbulae of the Coraciiformes (*sensu* Olson, 1985), whereas others are anisodactyl (or of unknown foot structure) and belong to at least three other higher taxa.

We collected numerous specimens of close relatives of *Eobucco* in the calcareous nodules of the Willwood Formation. A minimum of 10 individuals has now been prepared from six different nodules. Included as three-dimensional bones are every skeletal element except the prefrontal, vomer, maxilla, palatine, jugal arch, stapes, some vertebrae, metatarsal I, ribs, and phalanges. These are augmented by an articulated postcranial skeleton with feather impressions from the Lower Eocene Green River Formation, southwestern Wyoming (Fig. 1). It is this assemblage to which we address this paper.

Despite such good skeletal representation, it has proven very difficult to determine the phylogenetic relationships of the *Eobucco* assemblage because it has no close modern relatives. It shares some presumably primitive characters with several disparate orders of predominantly arboreal birds. The greatest number of similarities are shared with the family Coliidae (Coliiformes) (colies, or mousebirds) of Africa, an equally enigmatic group, whereas other characters suggest those of the suborder Pici (Piciformes) or even other orders. Our treatment of this fossil assemblage as a distinct order reflects our conclusion that these birds diverged from all other orders very early during the radiation of higher avian taxa.

MATERIALS AND METHODS

The following abbreviations of institutions are used in this paper: AMNH, American Museum of Natural History, New York; BMS, Buffalo Museum of Science, Buffalo, New York; UKVP, Museum of Natural History, University of Kansas, Lawrence; UM, Museum of Paleontology, University of Michigan, Ann

Arbor; UNSM, University of Nebraska State Museum, Lincoln; USNM, National Museum of Natural History, Washington, D.C.; UWGM, Geological Museum of the University of Wyoming, Laramie; YPM, Peabody Museum of Natural History, Yale University, New Haven, Connecticut.

Anatomical terminology follows Baumel (1979) and Vanden Berge (1979). Measurements are given in millimeters (mm).

Calcareous nodules from the Willwood Formation found at or near the surface of the ground were examined for external evidence of vertebrate fossils. Those exhibiting no fossils were broken into successively smaller fragments until fossils were found or until it was determined that no fossils were present. Damaged fossils were repaired with polyvinyl acetate, cyanoacrylate, or polyester laminating resin. The fossiliferous carbonate rock was slowly dissolved in a 7–12 percent solution of acetic acid for 2 days at a time. The treatment was repeated until the fossils were entirely free of the nodule. Between etchings, the nodules were rinsed for several hours in water and then air-dried, and the fossils were painted with a dilute solution of polyvinyl acetate dissolved in acetone. Small fragments of fossil bone were recovered by passing all discarded acid through a 0.59-mm mesh screen. One tibiotarsus was embedded in epoxy and prepared as a ground lapidary thin section, as described by Houde (1987). A specimen from the Green River Formation was prepared with a carbide needle under a dissecting microscope. Parts of this specimen were also repaired with polyester laminating resin and preserved with polyvinyl acetate. Fossil specimens were compared with the modern osteological material listed later. All specimens were drawn with the aid of a dissecting microscope. Most were drawn "free-hand" with the aid of measurements taken with dial calipers but not with a camera lucida. Drawings of paleotaxa are composites, made with reference to all available specimens, and usually are not of individual specimens, unless otherwise specified in the figure captions. No attempt was made to draw fractures or imperfections unless some aspect of the anatomy was entirely unknown. All appendicular elements illustrated are either from the right side or transposed so that they appear to be from the right side to facilitate comparisons.

COMPARATIVE OSTEOLOGICAL MATERIAL

All specimens are from the collection of the Division of Birds, Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA (USNM). Falconidae: *Falco sparverius* 555743; Opisthocomidae: *Opisthocomus hoazin* 344065; Glareolidae: *Rhinoptilus cinctus* 490230, *Cursorius coromandelicus* 432031; Psittacidae: *Forpus coelestis* 492387; Musophagidae: *Corythaeola cristata* 291079, *Tauraco livingstonii* 559413, *Tauraco persa* 291081; Cuculidae: *Clamator glandarius* 552920, *Urodynamis taitensis* 559589, *Eudynamys scolopacea* 490637, 292057, *Crotophaga major* 430932, *Piaya cayana* 558792, 492313, *Cuculus canorus* 490368, *Saurothera vieilloti* 501735, *Rhamphococcyx curvirostris* 559826, *Rhopodytes tristis* 431312, *Ceuthmochares aereus* 347410, *Coccyzus erythrophthalmus* 553126, *Guira guira* 345884, *Surniculus lugubris* 488329, *Morococcyx erythropygus* (partial skeleton) 361662, *Dromococcyx phasianellus* (partial skeleton) 347717, *Tapera naevia* 19221, *Geococcyx californicus* 555729, *Neomorphus geoffroyi* (partial skeleton) 347797, *Coua ruficeps* 432195, *Centropus senegalensis* 347407; Tytonidae: *Tyto alba* 553901; Strigidae: *Phodilus badius* 20310, *Ciccaba woodfordii* 491216, *Pseudoscops grammicus* 559185, *Pulsatrix perspicillata* 345889, *Rhinoptynx clamator* 347339, *Otus flammeolus* 554125, *Surnia ulula* 289974, *Asio otus* 554126, *Bubo virginianus* 559803, *Glaucidium brasilianum* 500519, *Ketupa ketupu* 559828, *Micrathene whitneyi* 555314, *Nyctea scandiaca* 491639, *Ninox novaeseelandiae* 492459, *Strix aluco* 559072, *Speotyto cunicularia* 501317, *Aegolius acadicus* 502238; Steatornithidae: *Steatornis caripensis* 560206; Podargidae: *Podargus strigoides* 492451; Nyctibiidae: *Nyctibius griseus* 555945; Aegothelidae: *Aegotheles cristatus* 227841; Caprimulgidae: *Podager nacunda* 344117, *Chordeiles acutipennis* 555588, *Nyctiprogne leucopyga* 429368, *Eurostopodus macrotis* 431310, *Nyctiphrynus ocellatus* 345891, *Caprimulgus carolinensis* 501321, *Phalaenoptilus nuttalli* 553912; Apodidae: *Streptoprocne semicollaris* 489351, *Cypseloides cherriei* 491750, *Cypseloides niger* 555770, *Hirundapus caudacutus* 500799, *Collocalia inexpectata* 489009, *Chaetura pelagica* 322320, *Cypsiurus parvus* 347445, *Tachornis phoenicobia* 553772, *Panyptila cayennensis* 431346, *Apus affinis* 431472, *Aeronautes andecolus* 227503; Hemiprocnidae: *Hemiprocne comata* 559923, *Hemiprocne longipennis* 226196; Trochilidae: *Glaucis hirsuta* 560156; Coliidae: *Urocolius macrourus* 499815, *Urocolius indicus* 558550, *Colius striatus* 558544, 558545; Trogonidae: *Priotelus temnurus* 429735, *Temnotrogon roseigaster* 318891, *Trogon melanurus* 347109, *Apaloderma narina* 430539, *Harpactes erythrocephalus* 557505, *Pharomachrus mocinno* 489405; Alcedinidae: *Alcedo quadribrachys* 291797, *Ceryle guttulata* 292776, *Dacelo novaeguieneae* 344389, *Halcyon funebris* 557210, *Tanysiptera galatea* 557230; Todidae: *Todus todus* 559190; Momotidae: *Momotus momota* 289783, *Electron platyrhynchum* 321526, *Baryphthengus ruficapillus* 559416; Meropidae: *Merops apiaster* 593064, *Nyctyornis amicta* 18766; Coraciidae: *Coracias caudata* 431907, *Eurystomus glaucurus* 430541; Leptosomidae: *Leptosomus discolor* 291845; Upupidae: *Upupa epops* 343282; Phoeniculidae: *Phoeniculus purpureus* 322395, *Rhinopomastus cyanomelas* 431715; Bucerotidae: *Tockus birostris* 347342, *Penelopides panini* 291383, *Anorrhinus galeritus* 18758, *Aceros cassidix* 224805; Galbulidae: *Jacamerops aurea* 430890, *Galbula galbula* 500436; Bucconidae: *Chelidoptera tenebrosa* 492224, *Nystalus chacuru* 321611, *Malacoptila panamensis* 432163, *Nonnula rubecula* 555954, *Monasa nigrifrons* 491483, *Notharchus macrorhynchos* 500432; Capitonidae: *Trachyphonus darnaudii* 320830, *Lybius torquatus* 558561, *Psilopogon pyrolophus* 558259, *Capito niger* 428698,

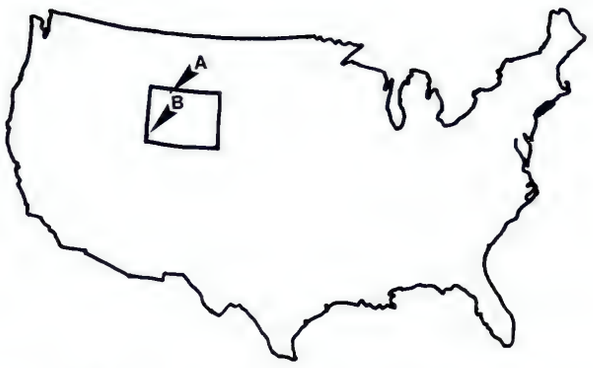

Figure 1. Map of the United States of America showing collecting localities in Wyoming (square). **A.** Localities of calcareous nodules in the Willwood Formation Sand Coulee area of the Bighorn Basin, Park County. **B.** Localities in the Green River Formation near Kemmerer, Lincoln County.

Tricholaema leucomelan 430550, *Megalaima virens* 431611, *Semnornis ramphastinus* 430761, *Calorhamphus fuliginosus* 344510, *Pogoniulus duchaillui* 291795, *Eubucco bourcierii* 560025, *Gymnobucco calvus* 347446; Indicatoridae: *Indicator indicator* 430329, *Prodotiscus insignus* 429686, *Melichneutes robustus* (partial skeleton) 430771; Ramphastidae: *Ramphastos vitellinus* 430217, *Pteroglossus torquatus* 346642, *Baillonius bailloni* 429862, *Aulacorhynchus sulcatus* 344099, *Selenidera maculirostris* 344870; Jyngidae: *Jynx torquilla* 603675; Picidae: *Dryocopus lineatus* 562567, *Dinopium benghalense* 346830, *Colaptes auratus* 554428, *Picus vittatus* 321099, *Dendropicos namaquus* 430385, *Melanerpes carolinus* 502631, *Veniliornis spilogaster* 558001, *Sphyrapicus varius* 502575, *Campephilus guatemalensis* 562569; Eurylaimidae: *Smithornis sharpei* 292424; Pittidae: *Pitta maxima* 557243; Scytalopodidae: *Rhinocrypta lanceolata* 227512; Formicariidae: *Thamnophilus punctatus* 428225, *Conopophaga castaneiceps* 559994; Cotingidae: *Ampelion rubrocristatus* 428910.

SYSTEMATIC PALEONTOLOGY

Sandcoleiformes new order

INCLUDED FAMILY. Sandcoleidae new family, the only known family in this order.

DIAGNOSIS. Distinguished from all sufficiently known orders of birds except Colliformes (colies) by the following combination of osteological characters.

Skull. Nostril holorhinal; postorbital and zygomatic processes very small; mandible with small symphysis.

Sternum. Carina shallow; posterior margin with four deep notches.

Vertebrae. Stout; many cervicals with osseous bridge connecting transverse process with posterior articular process, forming lateral accessory foramen; posterior cervicals and anterior thoracics with large pneumatic foramen in lateral surface of body; pygostyle very large, ventral process very large, and horizontal lumina projecting laterad from base.

Coracoid. Narrow except at sternal extremity.

Scapula. Acromion simple, without projections.

Humerus. Short and robust; large shallow depression for coracobrachialis muscle; bicipital crest pronounced and narrow; deltopectoral crest angular at midcrest, tapering distad to shaft, not angular distally; tricipital fossa single, without pneumatic foramen; lateral epicondylar process small but distinct; medial epicondyle pronounced medially, approximately equal in length to condyles.

Radius. Distal condyle large.

Ulna. Short, curved, without pronounced olecranon process or raised papillae for attachment of remiges.

Carpometacarpus. First metacarpal short; minor metacarpal bowed; intermetacarpal space wide; distal end truncate.

Femur. Head large; trochanteric crest low; condyles compressed obliquely forming a concavity on medial side, possibly for origin of m. femorotibialis internus; tuberosity for attachment of m. gastrocnemius lateralis and ansa of m. iliofibularis large and distinct.

Tibiotarsus. Cnemial crest low, broad, and pronounced proximomedially, anterior surface deeply concave, anterior crest continuing distad as pronounced ridge on medial aspect of shaft for origin of m. peroneus longus; condyles widely spaced, anteroposteriorly compressed, and well rounded in lateral view.

Tarsometatarsus. Approximately equal in length or slightly shorter than femur; shaft flattened proximally, cotylae widely separated; intercotylar eminence small and indistinct; hypotarsus very small and simple, very large, centrally positioned canal and a more medial tendinal groove, which may be divided in two; medial infracotylar foramen large; articular facet for metatarsal I facing mediad, trochleae II and IV narrow, elevated equally, and splayed outward; trochlea III wide and deeply grooved.

Pedal Phalanges. Robust; interphalangeal articulations very deeply grooved; claws sharply curved.

All members for which a given structure is known may be distinguished from the Coliiformes by having the following characters.

Skull. Internasal septum absent; quadrate without dorsally projecting process of lateral mandibular condyle; mandible more gracile, mandibular fenestra small or lacking.

Vertebrae. Thoracics without long ventral spines; pygostyle with horizontal lamella more ventral and not as pronounced.

Sternum. Sternocoracoid process shorter; spina externa of manubrium lamellate in midsagittal plane; intermediate trabecula arises from lateral trabecula and points caudomediad.

Furcula. Articulation of coracoid narrow.

Coracoid. Articulation of furcula larger, curved ventrally; sternal extremity wide, medial and lateral angles flared.

Humerus. Deltopectoral crest longer, broader, and more lamellate.

Radius and Ulna. Approximately equal in length to humerus.

Ulna. Dorsal cotylar process rounder; insertion of ventral collateral ligament smaller.

Carpometacarpus. Lacks intermetacarpal process.

Pelvis. Caudal iliac spine well developed; ischium longer, more slender.

Tibiotarsus. Anterior cnemial crest more pronounced; origin of m. femorotibialis internus elevated on distinct crater-shaped papilla; tendinal groove (extensor canal) positioned more medially; condyles smaller, widely separated.

Tarsometatarsus. Wider, flatter; without ossified extensor retinaculum; medial canal of hypotarsus enclosed (or imperfectly enclosed) with additional smaller groove posterolateral to it; facet for metatarsal I large and concave; trochleae II and IV more elevated and more splayed.

Pedal Phalanges. Claws strongly curved and robust, with large insertion of flexor tendon.

Sandcoleidae new family

INCLUDED GENERA. *Sandcoleus* new genus, *Anneavis* new genus, *Eobucco* Feduccia and Martin 1976, *Chascacocolius* new genus, and probably *Uintornis* Marsh 1872 and *Botauroides* Shufeldt 1915.

DIAGNOSIS. As for order.

DISTRIBUTION. Clarkforkian, Wasatchian and Bridgerian Land Mammal Ages, Early to Middle Eocene; Wyoming.

DESCRIPTION. In general, the species of the Sandcoleidae were small, arboreal, stocky, muscular birds. The foot was anisodactyl, facultatively zygodactyl, and possibly even facultatively pamprodactyl. The head was small, the wings and legs short, and the tail long. They probably resembled colies superficially, but they were larger and had a longer bill, such as that of a thrush (*Turdus* Linnaeus 1758). The following descriptions are made with reference to members of the higher landbirds (Olson, 1985), to which comparison is implied if not specified (e.g., "the head is small," meaning compared with the higher landbirds the head is small).

Skull (Fig. 2). The bill is of generalized proportions, neither

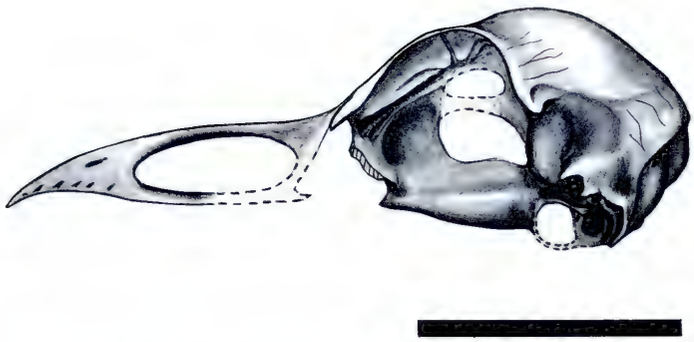

Figure 2. Reconstructed composite skull of *Sandcoleus copiosus* n. gen., n. sp., without palatal elements, left lateral aspect. Scale = 2 cm.

long nor short, heavy nor thin; the premaxillary symphysis is short; the nostril is large and holorhinal; the internarial septum and intranarial ossifications are absent; the cranium is nearly spherical; the pseudotemporal fossa is very shallow, the postorbital process very small, and the zygomatic process very small and conical, not flattened laterally, being just large enough to accept the lateral cotyla of the quadrate, as in *Tauraco* Kluk 1779. In the tympanic cavity, the osseous canal of the occipital ramus of the external ophthalmic artery is very large and conspicuous, extending between the two articular cotylae for the quadrate and across the middle of the dorsal pneumatic foramen, as in *Falco* Linnaeus 1758. The canal is a groove that does not appear to have been enclosed as an osseous tube in the tympanic cavity. The groove for the olfactory nerve is large and the medial orbitonasal foramen is paired, penetrating the ectethmoid medially as in *Falco*. The prefrontals are not fused with the frontals. The supraorbital region of the frontals is narrow and diverges anteriad to end in bilateral conical projections (that presumably articulate with the prefrontals and are not the prefrontals themselves). These projections are juxtaposed to a large

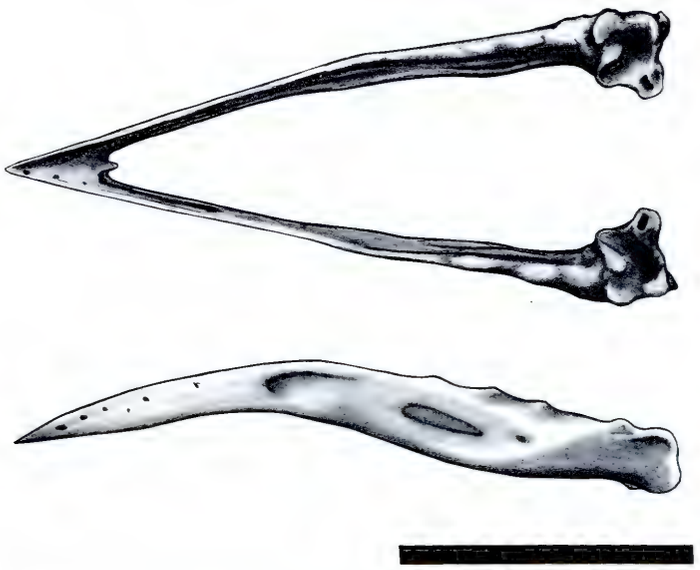

Figure 3. Reconstruction of the mandible of *Sandcoleus copiosus* n. gen., n. sp. (drawn from complete specimen in USNM 433973–434025 series). Upper: dorsal view; lower: left lateral aspect. Scale = 2 cm.

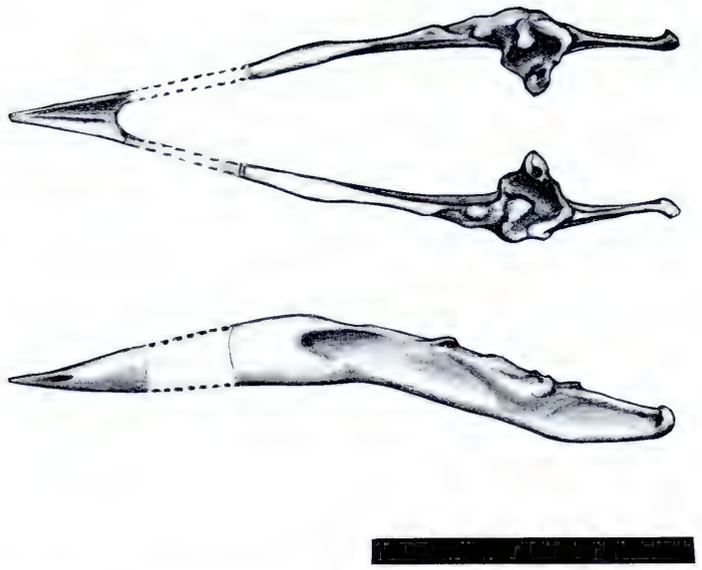

Figure 4. Reconstruction of the mandible of the holotype of *Chascacocolius oscitans* n. gen., n. sp. (USNM 433913, left side reconstructed from right). Upper: dorsal view; lower: left lateral aspect. Scale = 2 cm.

lateral orbitonasal foramen. Basipterygoid processes are absent. The pterygoid has flanges along its length, as in the Indicatoridae, and it is not cylindrical as in *Colius* Brisson 1760. The quadrate is similar to that of *Indicator* Stephens 1815, being stocky, with three well-defined mandibular condyles. The prootic and squamosal condyles are poorly separated and the orbital process is short. There are two large foramina on the medial surface of the quadrate that are separated by a well-defined ridge that connects the medial otic condyle with the medial mandibular condyle. The cotyla for the attachment of the quadratojugal includes a pit and a very small process projecting dorsad.

The mandible (Figs. 3, 4) is of medium length, with a very short mandibular symphysis, as in the Indicatoridae. The medial mandibular process is well developed but not long. The retroarticular process is developed to strikingly different degrees in different genera. Even when it is small, no more than a small ridge caudal to the lateral mandibular condyle, it is at least present, unlike in the Galbulae and Coraciiformes. The mandibular fenestra is small or absent. The dentary is slightly curved ventrally except at the rostral tip where the curvature is slightly dorsad. The mandible is superficially similar to that of the cuckoo *Eudynamys* Vigors and Horsfield 1826, except for the long retroarticular process in *Chascacocolius* new genus, which is described later.

The basihyal bone is short, broad, and basically hexagonal in dorsoventral view, with the apexes pointing laterad and with a ridge running anteroposteriad along the ventral surface.

Vertebrae. The vertebrae are stout, being similar overall to those in the Coliidae. Many of the cervicals have a tenuous osseous bridge connecting the transverse process with the posterior articular process, forming a lateral accessory foramen. The posterior cervicals and anterior thoracics have a large pneumatic foramen in lateral surface of body and lack long ventral spines. The caudal vertebrae have very long lateral and ventral spines. The pygostyle (Fig. 5) is very large, as in the Coliidae, but, unlike that of the Coliidae, the ventral process is very large

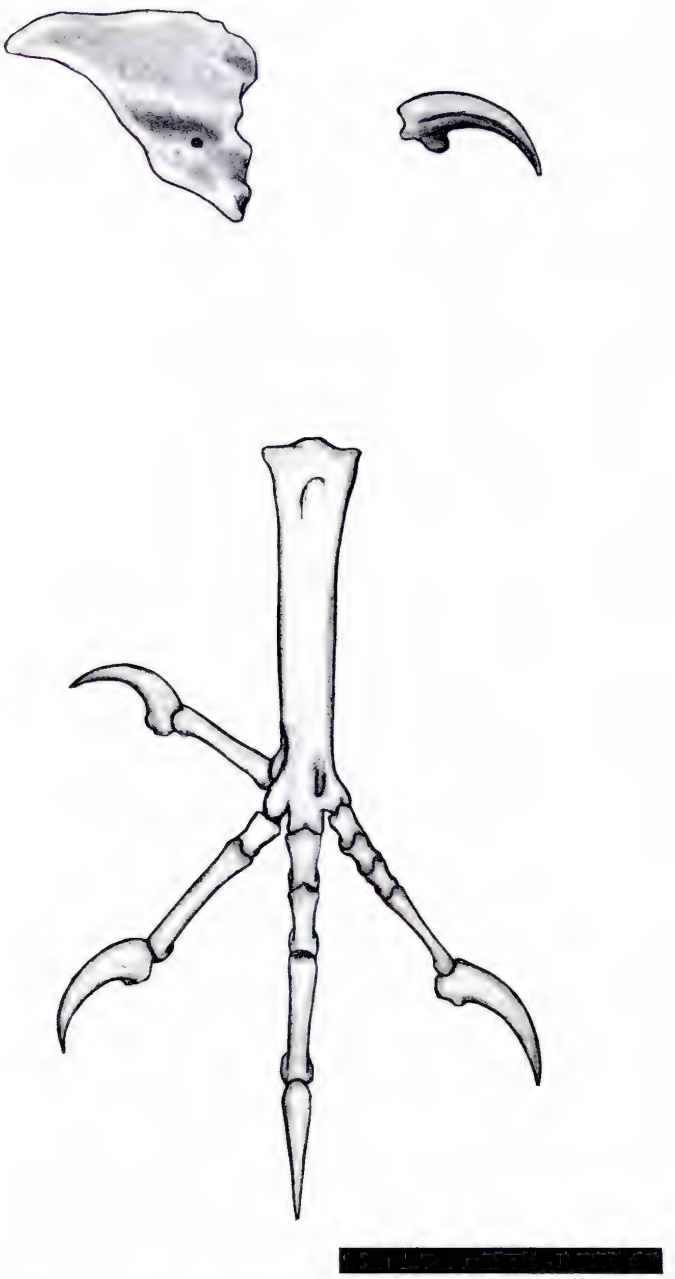

Figure 5. Upper left: right lateral aspect of the pygostyle of the holotype of *Sandcoleus copiosus* n. gen., n. sp. (USNM 433912); upper right: right lateral aspect of a terminal pedal phalanx of *S. copiosus;* lower: outline of the left pedal elements of the holotype of *Anneavis anneae* n. gen., n. sp. (BMS E 25337), showing the short proximal phalanges. Note that metatarsal I is unknown. Scale = 2 cm.

and the base is flat, as in a number of other families, e.g., Musophagidae.

Sternum. The sternum (Fig. 6) is longer than wide and is more expanded caudally, strongly resembling that in *Indicator* except for the manubrium. The manubrium is a well-developed single blade, rather than being bifid, and it protrudes anteriad from the carina, rather than being continuous with the carina as it is in *Indicator.* The carina is very shallow, the sternocoracoid processes are short, and the coracoidal sulci cross at the midline.

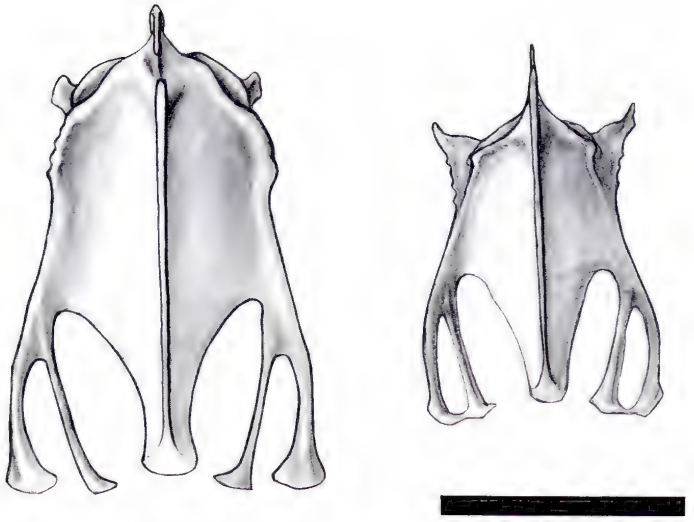

Figure 6. Reconstruction of the ventral aspect of the sternum. Left: holotype of *Sandcoleus copiosus* n. gen., n. sp. (USNM 433912); right: *Indicator indicator* (USNM 430329). Scale = 2 cm.

The costal margin is short and the caudal border has four deep notches, with the medial trabeculae originating from the lateral trabeculae, as in the Indicatoridae.

Furcula. The furcula is thin. Unlike most landbirds, it lacks a hypocleideum and the coracoidal articulation is small, without an articular facet.

Coracoid. The coracoid (Fig. 7) has a long, thin shaft. The cotyla for the scapula and the scapular extremity are very small and the procoracoid process is relatively small or absent, as in the Todidae and Momotidae. The furcular articulation is hooked ventromediad. The foramen of the supracoracoid nerve is inconspicuous. The sternal extremity is broad and curved, with a shallow depression in the region of m. sternocoracoideus and a very small depression medial to the line of m. supracoracoideus on the ventral surface of the sternal extremity. There is a distinct

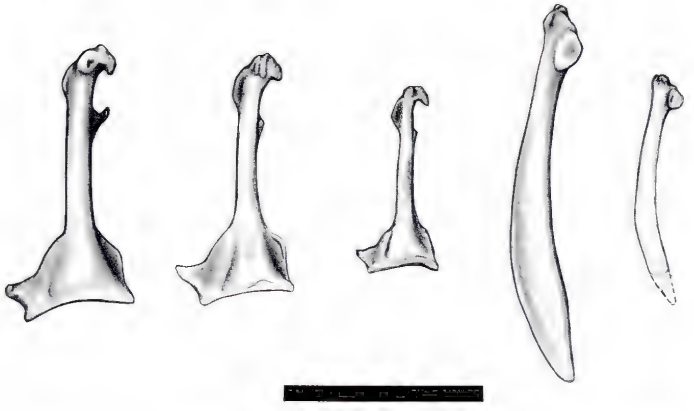

Figure 7. Reconstructions of the ventral aspects of the right coracoids and the dorsal aspect of the right scapulae of, from left to right, the coracoid of the holotype of *Sandcoleus copiosus* n. gen., n. sp. (USNM 433912), the coracoid of *Anneavis anneae* n. gen., n. sp. (composite reconstruction), the coracoid of the holotype of *Chascacocolius oscitans* n. gen., n. sp. (USNM 433913), the scapula of the holotype of *S. copiosus,* and the scapula of the holotype of *C. oscitans.* Scale = 2 cm.

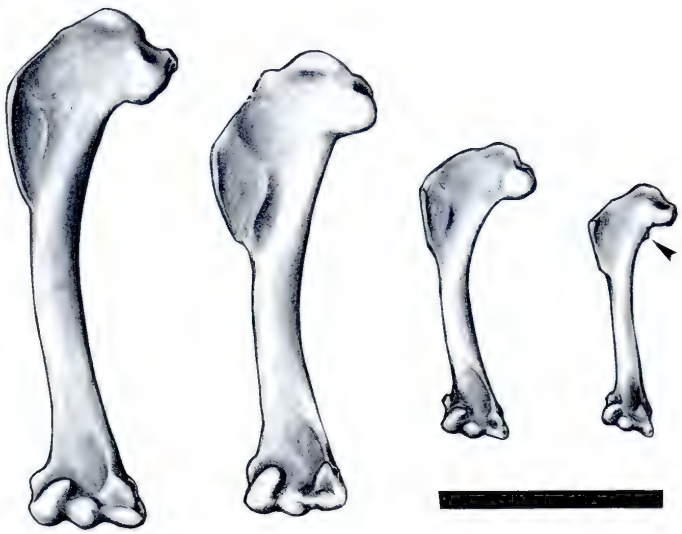

Figure 8. Reconstructions of the anterior aspects of the right humeri of, from left to right, respectively: the holotype of *Sandcoleus copiosus* n. gen., n. sp. (USNM 433912; reconstructed from right and left sides), *Anneavis anneae* n. gen., n. sp. (composite reconstruction), the holotype of *Chascacocolius oscitans* n. gen., n. sp. (USNM 433913; reconstructed from right and left sides), and *Colius striatus* (USNM 558544). Arrow: process, or "spur," of tricipital fossa; see text for details. Scale = 2 cm.

flange on the medial border of the sternal extremity. The lateral process is pronounced as in the Coraciidae and Musophagidae. The sternal articulation is not noticeable on the ventral surface.

Scapula. The scapula (Fig. 7) is simple and narrow. As in the Bucconidae and Trogonidae, there is no enlargement or process for an articulation with the furcula.

Humerus. The humerus (Fig. 8) is robust. The pectoral crest is large, pronounced, triangular, and lamellate, and it is nearly 30 percent as long as the entire bone. The coracobrachial depression is broad and shallow. The bicipital crest is very short, pronounced, and bulbous. The tricipital fossa is single, small, and deep, and it is not pneumatized. The shaft is robust and curved. The condyles and the medial epicondyle are bulbous, well rounded, and of approximately equal distal extent. The lateral epicondyle is a well-defined bump, positioned close to the radial condyle. The brachial depression is shallow, with an indistinct lateral border. The tricipital grooves are shallow. The humerus is most similar overall to that in the Coliidae except that the pectoral crest is more lamellate and lacks the process in the tricipital region of the coliid humerus (see Figs. 8, 9; this process has not been named to the best of our knowledge). There is also some resemblance to the humerus in the Trogonidae because of the long pectoral crest and short bicipital crest.

Ulna. The ulna (Fig. 10) is short, with a short, bulbous olecranon process. The shaft is curved in the proximal one-third to one-half, and its diameter may increase gradually from the midpoint to the distal end. There are no papillae for the attachment of secondary remiges.

Radius. The radius (Fig. 10) is short, straight, and robust, with a fairly large condyle.

Carpometacarpus. The carpometacarpus (Fig. 10) is short, with a pronounced extensor process and very short alular process. The intermetacarpal space is moderately wide as it is in *Coracias* Linnaeus 1758 and not as wide as in the Trogonidae. The intermetacarpal process is small or nearly absent. The minor metacarpal is slightly bowed, but not so extensively as in the Cuculidae, and the minor metacarpal often possesses a facet or buttress on the ventral surface for articulation with the ulnare. The articular facets for the digits are approximately equal in distal extent. The articular facet for the minor digit is a small, raised papilla.

Pelvis. The pelvis (Fig. 11) is wide, with the anterior and posterior portions of the ilium approximately equal in length. The anterior ala of the ilium does not meet the dorsal midline ridge of the synsacrum, and the terminal process of the ilium is present. The ala of the ischium, not including the terminal process, is approximately equal in length to the ilioischiadic foramen. The terminal process of the ischium is similar to that in *Indicator,* being very long, thin, and bent and ending in a large pedestal-like articulation with the pubis. The ischiopubic fenestra is very large, and the obturator foramen is also large, about equal in size to the acetabulum.

Femur. The femur (Fig. 12) is long, with a large head and low trochanteric crest. The cranial intermuscular line begins medial to the trochanteric crest, rather than on the crest. The lateral condyle is very large, and the medial condyle is small, with a concave medial surface. The tuberosity for the attachment of m. gastrocnemius lateralis and the ansa of m. iliofibularis are distinctly large, a diagnostic feature of the Sandcoleidae and Coliidae. The patellar groove is moderately deep, being very similar overall to the femur in *Colius,* except that the lateral condyle and associated structures are larger, and the condyles are compressed obliquely and rotated mediad relative to the shaft.

Tibiotarsus. The tibiotarsus (Fig. 13) is similar to that in the Coliidae and similar, but less so, to that in some of the Pici. The anterior cnemial crest is positioned far to the medial side. The lateral cnemial crest is large but not acute. The anterior and lateral cnemial crests are connected by a ridge that is exaggerated anteriorly but not proximally and that circumscribes a broad, concave intercristal "sulcus." The anterior cnemial crest is continuous distally with a ridge opposite the fibular crest. The origin of m. femorotibialis internus is elevated on a distinct papilla that has a concavity in it. The fibular crest is equal to or greater than one-third the length of the shaft and is more pronounced distally. The shaft curves mediad, especially at the level of the distal end of the fibular crest. The shaft diameter is narrowest at a level approximately two-thirds distad. The origin and insertion of the extensor retinaculum are pronounced. The extensor canal is positioned medially. The condyles are low, well rounded, and widely separated. The sulcus of the tibial cartilage is wide and shallow.

Tarsometatarsus. The tarsometatarsus (Figs. 14–16) is short, broad, and flat, with the cotylae widely separated. The intercotylar eminence is very low. The profile of the shaft becomes gradually narrower distally throughout its length until the level of the facet for the hallux. The hypotarsus is very small and low, being superficially similar to that in *Forpus* Boie 1858. There are three hypotarsal canals, two side by side and one behind, all centrally positioned between the cotylae. The lateral canal is the largest, and the medial and posterior canals may be connected as an imperfectly closed groove. The plantar surface of the shaft is relatively flat and does not form a large ridge as it meets the hypotarsus. The tuberosity of m. tibialis cranialis is large and positioned mediad, at a point distad one-third the length of the shaft. The infracotylar region is quite concave, with two large proximal vascular foramina. The facet for the hallux (=metatarsal I) is very large and faces mediad, not plantad.

Figure 9. Selected elements of the holotype of *Chascacocolius oscitans* n. gen., n. sp. (USNM 433913), above, compared with *Colius striatus* (USNM 558545), below. Left to right: posterior aspect of right humerus, posterior aspect of right radius, ventral aspect of right ulna, ventral aspect of left carpometacarpus, posterior aspect of left femur, and anterior aspect of right tibiotarsus (distal end of *Chascacocolius oscitans* not shown). Arrow: process, or "spur," of tricipital fossa; see text for details. Scale = 2 cm.

The interosseous foramen may be large or small. The distal (intertrochlear) foramen is large. Trochleae II and IV are elevated approximately equally and are splayed widely from trochlea III, so that the intertrochlear incisures are very wide. The trochleae lie in the same dorsoplantar plane. The collateral processes of trochleae II and IV are very large, particularly so in the latter, extending plantad to form a deep flexor trough, as in the Coliidae but more exaggerated. There is no sehnenhalter. Trochlea II is small and bulbous; trochlea III has a deep groove, and the medial ridge is smaller than the lateral ridge; and the medial ridge of trochlea IV in distal view forms a semicircle around the distal tendinal foramen, as in the Coliidae but more semicircular. The medial ridge of trochlea IV protrudes anteriad to form a groove medial to the trochlea on the anterior surface of bone distal to the interosseous foramen, as in the Coliidae.

Phalanges. The phalangeal formula is complete, and the phalanges are robust (Fig. 5). The three proximal phalanges of digit IV are extremely short as in the Coliidae, Apodidae, and Strigidae. The interphalangeal articular surfaces are highly convoluted as in the Strigidae. The plantar surfaces of the phalanges have bilateral ridges for the attachment of a ligamentous retinaculum. As in the Apodidae, the ungual phalanges are large and strongly hooked and have a large flexor tubercle; they are not bilaterally compressed.

Sandcoleus new genus

TYPE SPECIES. *Sandcoleus copiosus* new species, the type and only known species of this genus (see Fig. 19).

DIAGNOSIS. Placed in family by having the suite of characters listed previously for the Sandcoleidae.

Differs from *Anneavis* new genus by having: sternum with

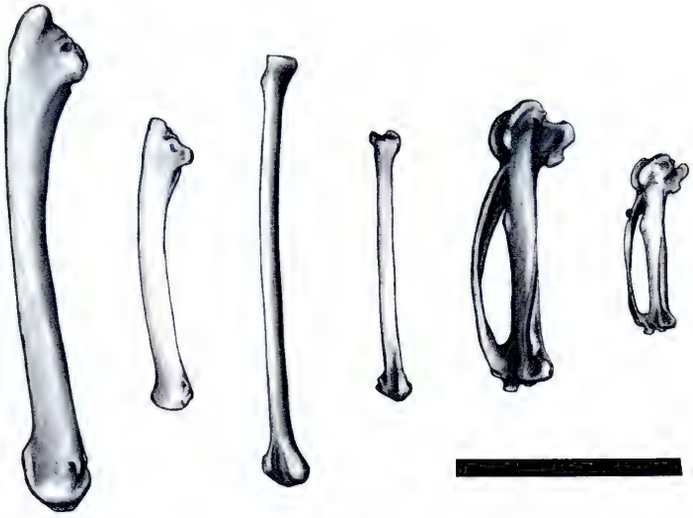

Figure 10. Reconstructions of the dorsal aspects of the right ulnae, the anterior aspects of the right radii, and the dorsal aspects of the right carpometacarpi, respectively. In each pair, right: *Sandcoleus copiosus* n. gen., n. sp. (composite reconstruction); and left: the holotype of *Chascacocolius oscitans* n. gen., n. sp. (USNM 433913; the left radius and carpometacarpus are reversed to appear to be the right side). Scale = 2 cm.

Figure 12. Reconstructions of the right femora of, from left to right: the dorsal aspect of *Sandcoleus copiosus* n. gen., n. sp. (composite reconstruction), the ventral aspect of the holotype of *Chascacocolius oscitans* n. gen., n. sp. (USNM 433913; left femur reversed to appear to be the right side), and the ventral aspect of *Colius striatus* (USNM 558544). Scale = 2 cm.

curved lateral margins; coracoid with long procoracoid process; humerus with narrower bicipital crest, longer medial epicondyle, pectoral crest pointing more palmad than laterad; preacetabular portion of pelvis longer; tibiotarsus with fibular crest not as pronounced distally, shaft of more uniform diameter throughout length; tarsometatarsus with larger distal vascular foramen, trochlea IV raised anteriorly with a groove medial to it on the anterior surface, trochlea III deeply grooved.

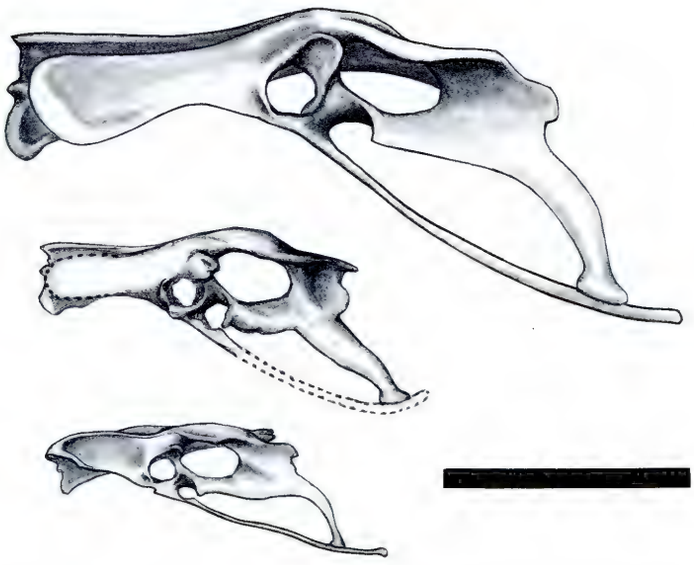

Figure 11. Reconstructions of the left aspects of pelves of, upper: the holotype of *Sandcoleus copiosus* n. gen., n. sp. (USNM 433912); middle: the holotype of *Chascacocolius oscitans* n. gen., n. sp. (USNM 433913); and lower: *Jynx torquilla* (USNM 603675). Scale = 2 cm.

Differs from *Eobucco* by having: tarsometatarsus with more bulbous trochleae II and IV in anterior view, trochlea III more nearly bilaterally symmetrical, lateral intertrochlear notch narrower, collateral flange of trochlea IV pointing plantad and not curved plantad–mediad around flexor tendons.

Differs from *Uintornis* by having: tarsometatarsus without ridge along medial margin of shaft, trochlea II and IV more elevated and bulbous in anterior view, trochlea III more bilaterally symmetrical.

Differs from *Chascacocolius* by having: tip of bill broader; mandible with a short, rather than long, retroarticular process; scapula with elongate glenoid facet; humerus with shorter pectoral crest and medial and lateral epicondyles shorter; radius with one groove in condyle, not two; carpometacarpus with very small intermetacarpal process, buttress for ulnare on minor metacarpal small or absent; pelvis with long anterior ala of ilium, no terminal iliac process, and terminal process of ischium more arched to create a wider ischiopubic fenestra; tibiotarsus with apex of proximal margin of cnemial crest more medial, fibular crest not as pronounced distally, distal aperture of extensor canal positioned in center of shaft in anterior view, no groove on anterior aspect of shaft medial to extensor canal.

ETYMOLOGY. A latinization of Sand Coulee, a river in the Clarks Fork Basin (northern Big Horn Basin), which is the namesake of both the fossiliferous Clarkforkian Sand Coulee beds of the Willwood Formation and the area from which all of the specimens of this genus have been collected. Coulee is a term widely used in western North America for a streambed, whether wet or dry. It is derived from French *couler,* to flow, and ultimately from Latin *colare,* to strain or sieve (cf. *colum,* a sieve). When thus latinized, the ending becomes a homophone of *Colius,* the living genus to which these birds are most similar. The generic name is to be treated as masculine in gender.

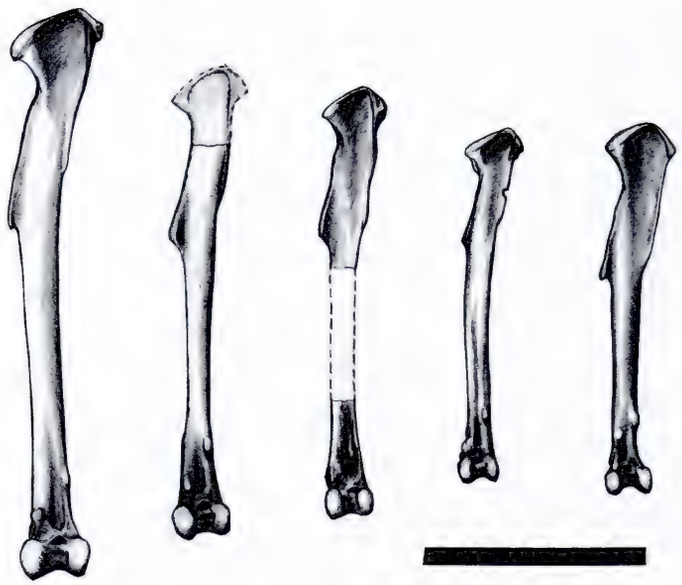

Figure 13. Reconstructions of the anterior aspects of the right tibiotarsi of, from left to right: *Sandcoleus copiosus* n. gen., n. sp. (USNM 433912), *Anneavis anneae* n. gen., n. sp. (composite reconstruction), the holotype of *Chascacocolius oscitans* n. gen., n. sp. (USNM 433913), *Colius striatus* (USNM 558544), and *Melanerpes carolinus* (USNM 502631). Scale = 2 cm.

Sandcoleus copiosus new species

HOLOTYPE. USNM 433912 (Figs. 17, 18), formerly articulated partial skeleton preserved in a calcareous nodule, lacking only the palatal elements, mandibular symphysis, some vertebrae and ribs, right carpometacarpus, right innominate, left tarsometatarsus, and some phalanges. Collected by A. Houde and P. Houde in July 1983.

Figure 14. Anterior aspects of the tarsometatarsi of, from left to right: *Sandcoleus copiosus* n. gen., n. sp. (composite reconstruction), the holotype of *Eobucco brodkorbi* Feduccia and Martin (UNSM 20046; left tarsometatarsus reversed to appear to be the right side), *Anneavis anneae* n. gen., n. sp. (composite reconstruction), *Uintornis lucaris* Marsh (referred specimen AMNH 8400; left tarsometatarsus reversed to appear to be the right side), and *Colius striatus* (USNM 558544). Scale = 2 cm.

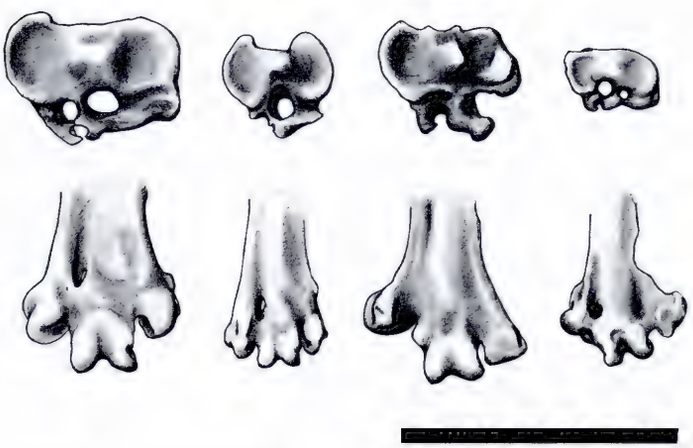

Figure 15. Tarsometatarsi. Upper row: proximal aspect; lower row, anterior aspect of trochleae; from left to right: *Anneavis anneae* n. gen., n. sp. (composite reconstruction), *Colius striatus* (USNM 558544), *Notharchus macrorhynchus* (USNM 500432), and *Forpus coelestis* (USNM 492387). Scale = 1 cm.

DIAGNOSIS. As for the genus.

TYPE LOCALITY. NW¼ of SE¼ Sec. 7, T56N R101W, Clark Quadrangle, Park County, Wyoming; 44°46′N, 109°23′W.

TYPE HORIZON. *Plesiadapis cookei* zone, Middle Clarkforkian (lowermost Eocene), Sand Coulee beds, Willwood Formation, Clark's Fork Basin.

REFERRED SPECIMENS. USNM 433973–434025, 53 elements representing a minimum of three individuals, including: complete crania (2), pterygoid, quadrate, mandible, coracoids (2), scapula, humerus, ulnae (2), carpometacarpus, femur and tarsometatarsi (2), incomplete cranium, quadrate, mandibles (2), sternum, coracoids (5), scapula, humeri (2), radii (2), ulnae (2),

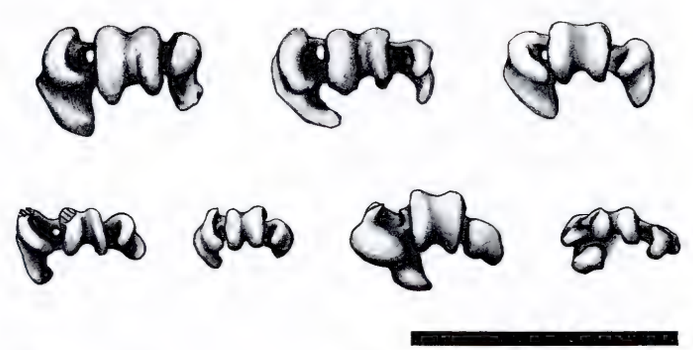

Figure 16. Reconstructions of the distal aspects of the tarsometatarsi of, upper row, from left to right: *Sandcoleus copiosus* n. gen., n. sp. (composite reconstruction), the holotype of *Eobucco brodkorbi* Feduccia and Martin (UNSM 20046), and *Anneavis anneae* n. gen., n. sp. (composite reconstruction); and lower row, from left to right: *Uintornis lucaris* Marsh (referred specimen AMNH 8400; left tarsometatarsus reversed to appear to be the right side), *Colius striatus* (USNM 558544), *Notharchus macrorhynchus* (USNM 500432), and *Forpus coelestis* (USNM 492387). Note that trochlea IV of *E. brodkorbi* is partially reconstructed; see text for details. Scale = 1 cm.

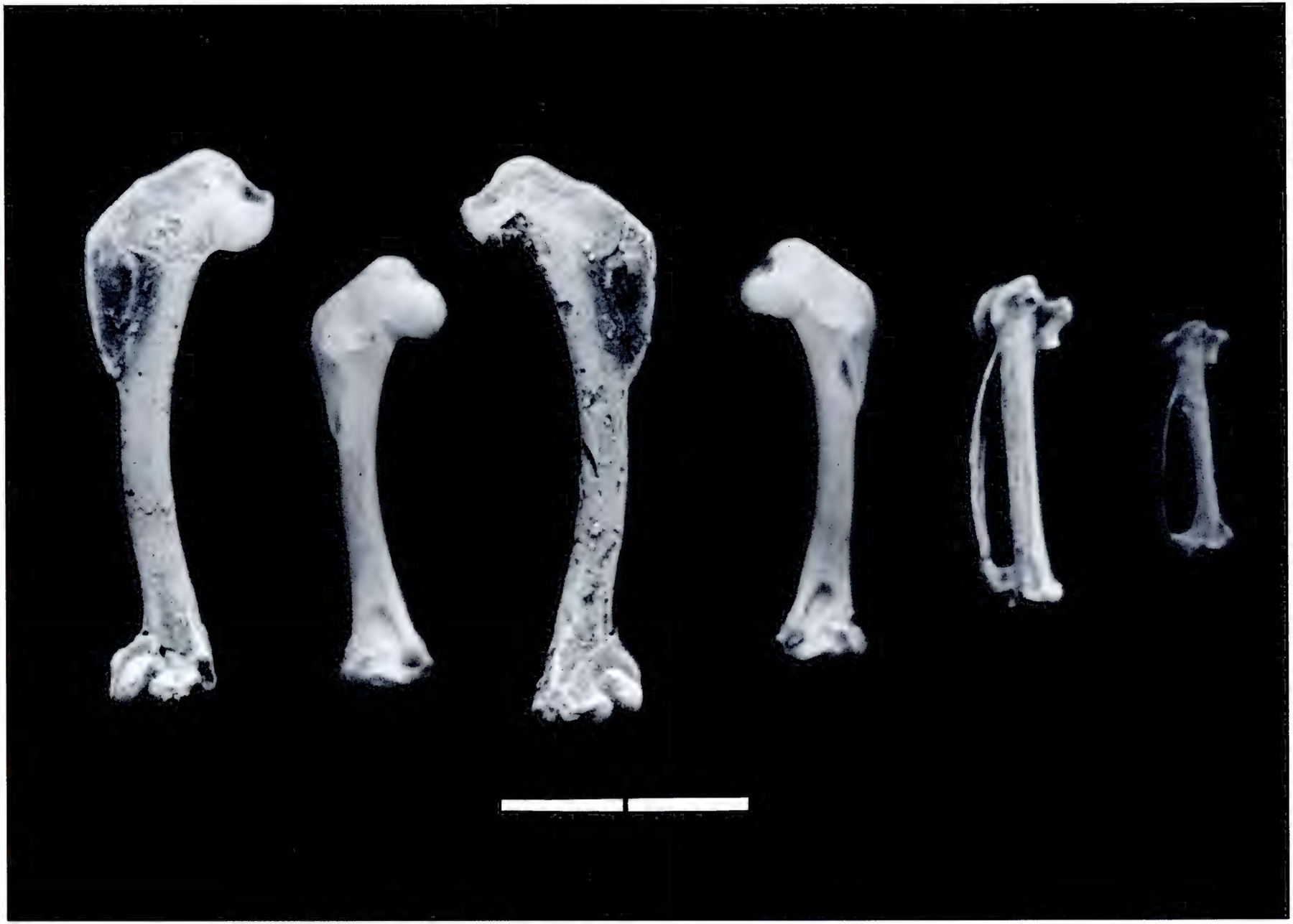

Figure 17. Selected elements of the holotype of *Sandcoleus copiosus* n. gen., n. sp. (USNM 433912), coated with ammonium chloride, compared with *Trogon* sp. (no data); from left to right: anterior aspect of right humerus of *S. copiosus*, right humerus of *Trogon* sp., left humerus of *S. copiosus*, and left humerus of a trogon, and dorsal aspect of: right carpometacarpus of *S. copiosus* and right carpometacarpus of a trogon. Scale = 2 cm.

Figure 18. Selected elements of the holotype of *Sandcoleus copiosus* n. gen., n. sp. (USNM 433912), coated with ammonium hydroxide, compared with *Colius striatus* (USNM 558545); from left to right: anterior aspect of left tibiotarsus of *S. copiosus*, left tibiotarsus of *C. striatus*, right tarsometatarsus of *S. copiosus*, and right tarsometatarsus of *C. striatus*. Scale = 2 cm.

carpometacarpus, femur and tibiotarsus, and assorted tracheal rings, vertebrae, a pygostyle, phalanges, and fragments all preserved in one calcareous nodule, collected by A. Houde and P. Houde from NE¼ of SE¼ Sec. 7, T56N R101W, Clark Quadrangle, Park County, Wyoming; 44°46′N, 109°23′W; Middle Clarkforkian Land Mammal Age.

UM 83893, formerly articulated partial skeleton, including: partial quadrate, humerus, radius, ulna, pelvis, femora, tibiotarsi, tarsometatarsus, and assorted vertebrae and fragments preserved in a calcareous nodule, collected by A. Houde and P. Houde from NE¼ of SE¼ Sec. 7, T56N R101W, Clark Quadrangle, Park County, Wyoming; 44°46′N, 109°23′W; Middle Clarkforkian Land Mammal Age.

USNM 433914–433917, four elements representing a minimum of one individual, including: coracoid, the distal end of a humerus, carpometacarpus, and the proximal end of a tibiotarsus, all preserved in one calcareous nodule, collected by A. Houde and P. Houde from NE¼ of NE¼ Sec. 5, T56N R101W, Clark Quadrangle, Park County, Wyoming; 44°46′N, 109°23′W; Early Wasatchian Land Mammal Age.

USNM 433971 and 433972, carpometacarpus and proximal end of a femur preserved in a calcareous nodule, collected by

Figure 19. Hypothetical restoration of *Sandcoleus copiosus* n. gen., n. sp., an abundantly preserved species in calcareous nodules from the Early Eocene Willwood Formation of Wyoming.

A. Houde and P. Houde from NW¼ of SE¼ Sec. 23, T56N R102W, Clark Quadrangle, Park County, Wyoming; 44°46′N, 109°23′W; Early Wasatchian Land Mammal Age.

ETYMOLOGY. Latin, *copiosus*, abundant, in allusion to the frequency of occurrence of this species in calcareous nodules in the Sand Coulee area.

DISTRIBUTION. Clarkforkian and Wasatchian Land Mammal Ages of the Willwood Formation in Clark's Fork Basin, Wyoming.

COMMENTS. All referred material was collected in and near the type locality. There is remarkable heterogeneity in morphology, even among individuals from the type locality. In particular, two tarsometatarsi from the same nodule differ from one another in the sizes of the proximal and distal vascular foramina, the degree of concavity of the plantar surface, and the width of the shaft. A tarsometatarsus from a different nodule is morphologically similar to one of the two, but it is somewhat larger. We attribute these differences to individual, rather than interspecific, variation.

Numerous referred specimens (USNM 433973–434025) representing a minimum of three individuals were recovered from the same calcareous nodule as the holotypes of *Lithornis promiscuus* Houde 1988 and *Lithornis plebius* Houde 1988. These specimens of *Sandcoleus* were mistakenly referred to as *Eobucco* sp. in the description of *L. promiscuus* (Houde, 1988:37).

Sandcoleus copiosus was synchronous and sympatric with *Anneavis anneae* in the Early Wasatchian of the Clark's Fork Basin.

Sandcoleus copiosus is larger than all other known members of this family except *Eobucco brodkorbi*, which it equals in size.

MEASUREMENTS (mm) OF HOLOTYPE. Left and right, respectively, are given for paired elements when both are present.

Skull. Length, 52.0; width of premaxillae at anterior margin of nostril, 6.0; breadth across zygomatics, 20.1; supraorbital width, 7.6.

Mandible. Length of internal process from lateral cotyla, 7.3, 7.3; width of cotylae, 5.5, 5.5; depth of mandible, 5.0, 4.8.

Sternum. Length, 41.2; width at costal margin, 19.4; width at caudolateral process, 26.1; depth of carina from coracoidal sulci, 11.6.

Coracoid. Length, 24.4, 24.7; width of sternal articulation, —, 10.4; length of procoracoid, 4.4, 4.3; width of glenoid facet, 2.7, 2.7; width of midshaft, 2.2, 2.3.

Scapula. Length, 38.1, 37.7; width of shaft, 3.0, 3.3; width of glenoid facet, 2.6, 2.6.

Humerus. Length, 46.3, 45.6; length of pectoral crest from caput, 20.5, 20.4; length of bicipital crest from caput, —, 9.7; diameter of midshaft, 4.1, 4.0; distal width, 10.0, —; depth of condyles, 5.1, —.

Radius. Length, 41.2, 41.6; proximal width, 3.7, 3.7; diameter of midshaft, 1.9, 1.7; distal width, 4.7, 4.6.

Ulna. Length, 45.2, 45.4; maximum proximal width, 6.6, 6.8; diameter of midshaft, 3.5, 3.4; width of condyle, 4.9, 5.0; depth of condyle, 5.5, 5.6.

Carpometacarpus (Left). Length, 25.9; width of trochlea, 4.2; length from alular process to extensor process, 4.4; height of extensor process from trochlea, 7.6; anteroposterior width of midshaft of major metacarpal, 2.3; intermetacarpal width, 2.3; width of articular facet for major digit, 3.0.

Pelvis. Length of synsacrum, 35.6; width of body of synsacrum, 6.0; estimated width across antitrochanters, 25.4; length of anterior ala of ilium from acetabulum, 20.5; length of posterior ala of ilium from acetabulum, 17.9; length of ischium from acetabulum, 24.0.

Femur. Length, 36.7, 36.5; length of head from trochanteric crest, 7.6, 7.8; diameter of head, 3.4, 3.4; height of trochanteric crest, 5.2, 4.7; diameter of midshaft, 3.1, 3.1; distal width, 7.7, 7.8; height of medial condyle, 4.3, 4.4; height of lateral condyle and tibiofibular crest, 5.9, 5.8.

Tibiotarsus. Length (from articular surfaces, not cnemial crest), 50.1, 50.9; width of cnemial crest, 8.0, —; width of proximal articular surface, 6.1, 6.0; proximal depth (cnemial crests to condyles), 7.7, —; length of fibular crest from proximal condyles, 18.2, —; height of fibular crest, 4.6, —; maximum width of midshaft, 3.0, 3.0; distal width, 6.2, 6.1; depth of medial condyle, 4.8, —; depth of lateral condyle, —, 4.8.

Tarsometatarsus (Right). Length, 28.1; proximal width, 6.8; proximal depth, 5.2; width of midshaft, 3.3; depth of midshaft, 2.1; depth of trochlea II, 2.7; depth of trochlea III, 2.9; width of trochlea III, 2.8; depth of trochlea IV, 4.0.

Pygostyle. Maximum length, 17.7; maximum width, 5.4.

Anneavis new genus

TYPE SPECIES. *Anneavis anneae* new species, the type and only known species of this genus.

DIAGNOSIS. Placed in family by having the suite of characters listed previously for Sandcoleidae.

Differs from *Sandcoleus* by having the characters mentioned for *Anneavis* in the diagnosis of the former genus.

Differs from *Eobucco* by having: tarsometatarsus with more bulbous trochleae II and IV in anterior view, trochlea III more nearly bilaterally symmetrical, lateral intertrochlea notch narrower, collateral flange of trochlea IV pointing plantad and not curved plantad–mediad around flexor tendons.

Differs from *Uintornis* by having: tarsometatarsus without ridge along medial margin of shaft, with trochlea II and IV more elevated and bulbous in anterior view, trochlea III more bilaterally symmetrical.

Differs from *Chascacocolius* by having: tip of bill broader; scapula with elongate glenoid facet; humerus with shorter pectoral crest, and medial and lateral epicondyles shorter; radius with one tendinal groove, not two; carpometacarpus with very small intermetacarpal process, buttress for ulnare on minor metacarpal smaller; tibiotarsus with distal aperture of extensor canal positioned in center of shaft in anterior view, and no groove on anterior aspect of shaft medial to extensor canal.

ETYMOLOGY. *Anne,* plus Latin, *avis,* a bird. The genus and type species are dedicated to Anne E. Houde, for assisting in the discovery and collection of every specimen from the Willwood Formation included in this paper. The generic name is feminine in gender.

Anneavis anneae new species

Figures 20, 21

HOLOTYPE. BMS E 25337, postcranial skeleton with feather impressions on a marlstone slab. Collected by Verl and Rick Hebdon.

DIAGNOSIS. As for genus.

TYPE LOCALITY. Warfield fossil quarries at Warfield Springs, near Kemmerer, Lincoln County, Wyoming, NW¼ Sec. 5, T19N R117W; 41°44′N, 110°31′W.

TYPE HORIZON. Upper Wasatchian (Lower Eocene), Fossil Butte Member of the Green River Formation, from a "blue layer" about 30–45 cm thick underlying a thick layer of cream-colored calcareous sediment. This is one of the "F-2" localities in the Eocene Fossil Lake mentioned by Grande (1984:13, fn.).

REFERRED SPECIMENS. USNM 336571, 433934–433970, 38 elements representing a minimum of three individuals, including: complete quadrate, coracoids (2), scapula, humerus, ulna, and tarsometatarsi (2), incomplete premaxilla, cranium, sternum, scapulae (2), humeri (5), radius, synsacrum, femur, tibiotarsi (3), and assorted vertebrae, phalanges, and fragments all preserved in one calcareous nodule, collected by A. Houde and P. Houde, from NW¼ of SE¼ Sec. 23, T56N R102W, Clark Quadrangle, Park County, Wyoming; 44°46′N, 109°23′W; Early Wasatchian Land Mammal Age.

USNM 433918–433933, 16 elements representing a minimum of two individuals, including: coracoids (2), humeri (2), carpometacarpi (2), synsacrum and tarsometatarsi (3), and incomplete sternum, femur, tibiotarsus, and phalanges, all preserved in one calcareous nodule, collected by A. Houde and P. Houde from NE¼ of NE¼ Sec. 5, T56N R101W, Clark Quadrangle, Park County, Wyoming; 44°46′N, 109°23′W; Early Wasatchian Land Mammal Age.

UWGM 20312, a partial articulated skeleton from the Split Fish layer, Fossil Butte Member, Green River Formation, Lincoln County, Wyoming.

DISTRIBUTION. Early to Late Wasatchian; Willwood and Green River Formations, Wyoming.

COMMENTS. The clearly visible feather impressions of the holotype reveal that *Anneavis anneae* possessed short remiges and a very long, tapered tail, like that of the Coliidae (Fig. 21). The long rectrices may have been present in all members of the family. The only other genus of this family in which the pygostyle is known is *Sandcoleus,* in which it is large. From this it is assumed that its rectrices were long.

Numerous referred specimens of *Anneavis anneae* (USNM 336571, 433934–433970) were recovered from a calcareous nodule that also contained specimens of lithornithids, a flightless predatory bird, an artiodactyl and other mammals, and a lizard. The midshaft of the tibiotarsus of one of these referred specimens (USNM 336571) was embedded in epoxy and prepared as a polished lapidary thin section by Houde (1987:126), who erroneously referred to the specimen as "*Eobucco* sp."

This species is most similar to *Sandcoleus copiosus* and *Eobucco brodkorbi* among known sandcoleids and was sympatric with the former in the Early Wasatchian in the Clark's Fork Basin, Wyoming.

This species is smaller than *Eobucco brodkorbi* or *Sandcoleus copiosus* and larger than *Uintornis lucaris* or *Chascacocolius oscitans.*

MEASUREMENTS (mm) OF HOLOTYPE. Left and right, respectively, are given for paired elements when both are present.

Sternum. Length, ca. 39; width at costal margin, 19.1; width at caudolateral process, ca. 31.

Coracoid. Length, 23.2, 22.8; length of sternal articulation, —, ca. 9.7; width of midshaft, ca. 2.4, —.

Humerus. Length, 41.7, 40.1; length of pectoral crest from caput, 18.8, 18.8; length of bicipital crest from caput, 8.1, 8.1; diameter of midshaft, 3.8, 4.6; distal width, —, ca. 7.5.

Radius. Length, 37.0, 38.2; diameter of midshaft, 1.9, 1.6.

Ulna. Length, —, 41.5; diameter of midshaft, 3.8, 4.4.

Carpometacarpus. Length, 21.6, 22.8; length from alular process to extensor process, 4.4, 4.9; height of extensor process from trochlea, 7.3, 7.7; anteroposterior width of midshaft of major metacarpal, 2.0, 1.6; intermetacarpal width, 1.9, 2.1.

Pelvis. Length of synsacrum, 26.9; width of body of synsacrum, 7.7; width through acetabula, 20.7; length of ischium from acetabulum, ca. 17.5, 16.

Femur. Length, 27.7, 33.4; diameter of midshaft, 2.8, 2.8.

Tibiotarsus. Length (cnemial crest–condyles), 43.3, 40.4; width of cnemial crest, 6.5, —; height of fibular crest (diameter of shaft plus elevation of ridge), 4.1, —; maximum width of midshaft, 2.7, —; distal width, 5.3, —; depth of medial condyle, —, 3.7.

Tarsometatarsus. Length, 23.7, 23.5; proximal width, 5.8, 5.9; width of midshaft, 3.1, 3.3; depth of trochleae, 6.2, 4.8; width of trochlea III, 2.2, —.

Pygostyle. Maximum length, 15.1

Eobucco Feduccia and Martin 1976

INCLUDED SPECIES. *Eobucco brodkorbi;* the type and only known species of this genus.

EMENDED DIAGNOSIS. Placed in order by having the suite of tarsometatarsal characters listed previously for Sandcoleiformes. Differs from all sufficiently known members of the family in which the tarsometatarsus is known by having: wider lateral

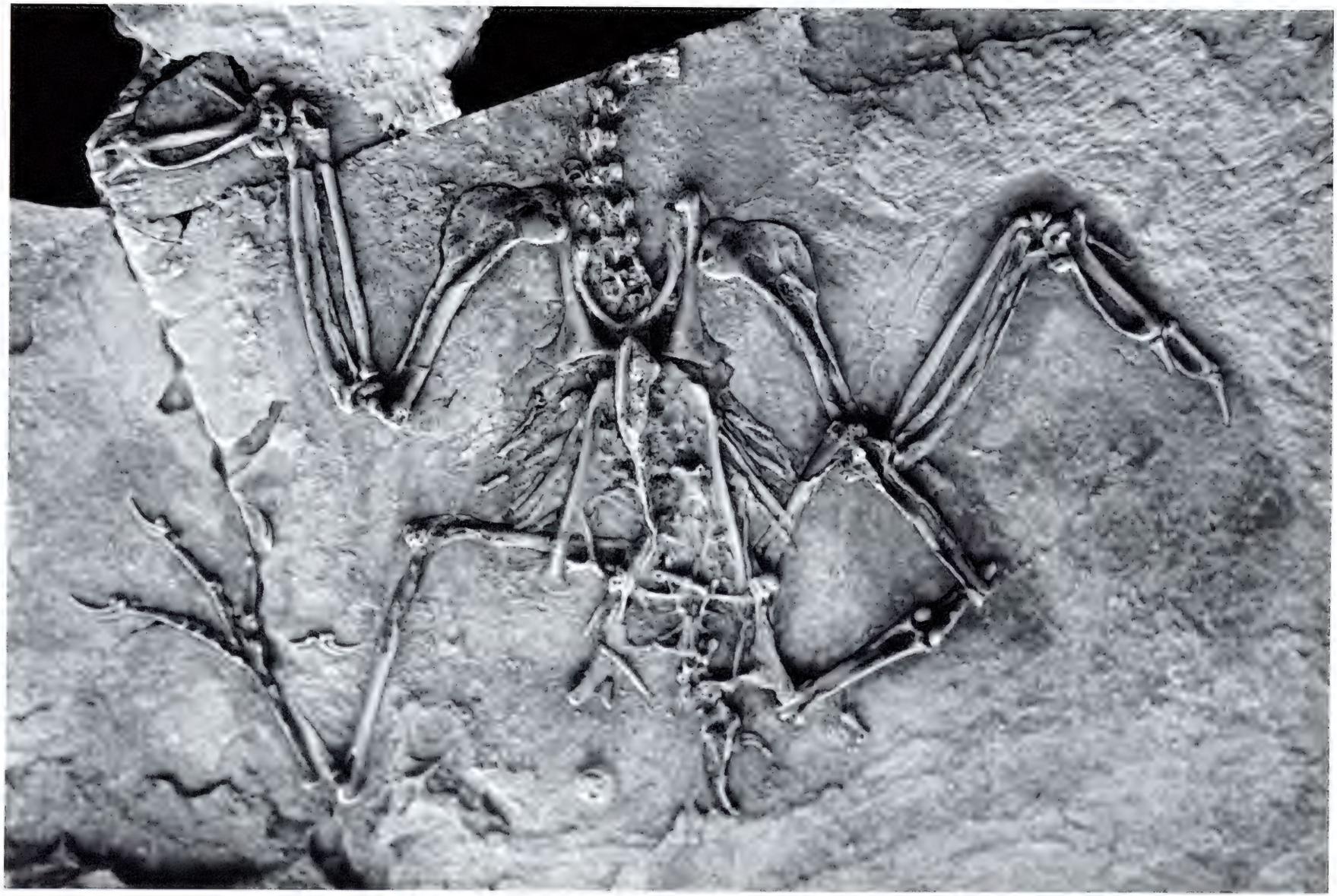

Figure 20. Holotype of *Anneavis anneae* n. gen., n. sp. (BMS E 25337), from the Lower Eocene Green River Formation of Wyoming. The specimen consists of the postcranial skeleton. It is coated with ammonium chloride to enhance details of the bones, but this obscures the feather impressions.

Figure 21. Holotype of *Anneavis anneae* n. gen., n. sp. (BMS E 25337), from the Lower Eocene Green River Formation of Wyoming, showing impressions of the feathers. The pencil points to the lateral margin of the tail feathers.

intertrochlear notch and collateral flange of trochlea IV bent more mediad around flexor tendons.

Differs from *Sandcoleus* and *Anneavis* by having: tarsometatarsus with less concave plantar surface, narrower trochleae II and IV, and trochlea III asymmetrical with medial ridge smaller than lateral ridge. Also differs from *Anneavis* by having: trochlea IV raised anteriad and with groove medial to it on anterior surface of shaft.

Differs from *Uintornis* by having: tarsometatarsus without ridge along medial border of shaft, trochleae II and IV more elevated, and with narrower lateral intertrochlear notch.

Eobucco brodkorbi Feduccia and Martin 1976

Figures 14, 16

HOLOTYPE. UNSM 20046, left tarsometatarsus.

EMENDED DIAGNOSIS. As for genus.

TYPE LOCALITY. "56 km north of Green River, Sweetwater County, Wyoming" (Feduccia and Martin, 1976).

TYPE HORIZON. "Bridger Formation, Middle Eocene" (Feduccia and Martin, 1976).

REFERRED SPECIMENS. None

COMMENTS. We find certain inaccuracies in the original description of this species by Feduccia and Martin (1976:109), which reads as follows: "... intercotylar eminence high and large; hypotarsus damaged but with a large lateral square of bone, which may have included a closed canal (the two closed canals, such as found in cuculids, could not have been present) ... tubercle for tibialis anticus very small and distally situated along the medial edge of shaft ..." Compared to birds that possess a high and large intercotylar eminence, such as in the Pici, the eminence of *Eobucco* is very low. The hypotarsus in the holotype of *E. brodkorbi* is indeed broken; nonetheless, we believe that it possessed two or three closed canals as in the other members of the family. A large proximomedial fragment of the holotype is missing, including everything medial to the insertion of m. tibialis anticus and the medial proximal vascular canal. In their illustration of the holotype, Feduccia and Martin (1976: fig. 6) included a dashed line from the intact medial margin of the shaft proximad to the damaged tubercle for m. tibialis anticus and incorrectly indicated this to be the medial border of the tarsometatarsus. The tubercle for insertion of m. tibialis anticus is large, not small, and is not positioned on the medial edge of the shaft. Our illustrations (Figs. 14, 16) correct this and two other matters of reconstruction. The anterior surface of trochlea IV is damaged and probably would have been similar to that of *Sandcoleus* or *Colius*. The lateral flange of trochlea IV is cracked and flattened against the shaft but probably would have been positioned more plantad, as shown in our drawing.

Eobucco brodkorbi is larger than all other sufficiently known members of the family except *Sandcoleus copiosus*, to which it is equal in size.

Uintornis Marsh 1872

INCLUDED SPECIES. *Uintornis lucaris* Marsh 1872, type species, and *Uintornis marionae* Feduccia and Martin 1976 (this species was not examined).

EMENDED DIAGNOSIS. Placed in order by having the suite of tarsometatarsal characters listed previously for Sandcoleiformes.

Differs from all sufficiently known members of the family by having: tarsometatarsus with narrower shaft, ridge along medial edge of shaft, trochlea III markedly asymmetrical with lateral ridge much larger than medial ridge and lateral intertrochlear notch very wide anteriorly.

Uintornis lucaris Marsh 1872

HOLOTYPE. YPM 617, distal end of right tarsometatarsus.

DIAGNOSIS. As for genus; *Uintornis marionae* not examined; see Feduccia and Martin (1976).

TYPE LOCALITY. Henry's Fork, Sweetwater County, Wyoming.

TYPE HORIZON. Bridger Formation, Middle Eocene.

REFERRED SPECIMENS. AMNH 8400 (Figs. 14, 16), distal end of left tarsometatarsus.

COMMENTS. *Uintornis* has been treated as a woodpecker, a puffbird, a cuckoo, and a primobucconid (taxonomic history reviewed by Feduccia and Martin, 1976). Because this species is known from only a fragment of a single element, we cannot be certain that it is properly included in the Sandcoleidae. It is consistent with other members of the family by having: tarsometatarsus with facet for metatarsal I facing mediad, not plantad, inner ridge of trochlea IV roughly semicircular in distal view, lateral flanges of trochlea II and especially trochlea IV exaggerated posteriorly, all of which suggest that *Uintornis* was facultatively zygodactyl and pamprodactyl, as were other sandcoleids.

Uintornis marionae Feduccia and Martin 1976

HOLOTYPE. UKVP 26906, distal end of right tarsometatarsus.

DIAGNOSIS. Not examined; see Feduccia and Martin (1976).

TYPE LOCALITY. Sage Creek, Sweetwater County, Wyoming.

TYPE HORIZON. Bridger Formation, Middle Eocene.

REFERRED SPECIMENS. None.

COMMENTS. Although we have not examined this species, it appears to have been correctly identified by Feduccia and Martin (1976) as a congener of *U. lucaris*.

Chascacocolius new genus

TYPE SPECIES. *Chascacocolius oscitans* new species, the type and only known species of the genus.

DIAGNOSIS. Placed in family by having the suite of characters listed previously for the Sandcoleidae. Differs from all members of the family for which a given structure is known by having: mandible with narrow symphysis and long retroarticular process; scapula with rounder glenoid facet; humerus with larger pectoral crest, long medial and lateral epicondyles; radius with two tendinal grooves, one in dorsal edge of distal extremity; carpometacarpus with pronounced buttress for ulnare located on ventral surface of minor metacarpal, larger intermetacarpal process, minor metacarpal less bowed; pelvis with well-developed terminal iliac process, large ilioischiadic foramen, smaller ilioischiadic lamina, obturator foramen large and nearly enclosed, and straighter terminal process of ischium; femur with larger papilla for attachment of m. gastrocnemius lateralis and ansa of m. iliofibularis, and more excavated medial aspect of medial condyle; tibiotarsus with proximal apex of profile of cnemial crest more lateral, intercristal sulcus shallower, groove medial to extensor canal on anterior surface of distal end, distal aperture of extensor canal more medial. Also differs from *Sandcoleus* by having: coracoid with short procoracoid process.

ETYMOLOGY. Greek *chaskax, chaskakos,* a gaper, plus the generic name *Colius,* which is supposed to derive ultimately (see Newton, 1896:101) from Greek *kolios,* a jackdaw. The name is masculine in gender and refers to the strong gaping adaptations evident in the mandible.

Chascacocolius oscitans new species

HOLOTYPE. USNM 433913 (Fig. 9), formerly articulated partial skeleton, including the mandible, right quadrate, basihyal, several cervical and thoracic vertebrae, furcula, right and left coracoid, right scapula, right and left humerus, right ulna, left radius and distal half of right radius, left carpometacarpus, pelvis lacking right innominate, left femur, right tibiotarsus, and a few phalanges. Collected in a calcareous nodule by A. Houde and P. Houde in July 1985.

DIAGNOSIS. As for genus.

TYPE LOCALITY. NW¼ of NE¼ Sec. 4, T55N R101W, Clark Quadrangle, Park County, Wyoming; 44°46′N, 109°23′W.

TYPE HORIZON. Lower Wasatchian (Lower Eocene), Gray Bull beds, Willwood Formation, Clark's Fork Basin.

REFERRED SPECIMENS. None.

ETYMOLOGY. Latin, *oscitans,* gaping, yawning, again in reference to the gaping adaptation of the species.

DISTRIBUTION. Early Wasatchian Land Mammal Age of the Willwood Formation in Clark's Fork Basin, Wyoming.

COMMENTS. Both this genus and *Uintornis* are widely divergent from the other members of the family (*Botauroides* is excluded from consideration here) and also include the smallest species yet discovered. *Uintornis* is known only from the tarsometatarsus, which is unfortunately the only major appendicular element that remains unknown for *Chascacocolius.* Thus, it is possible that *Chascacocolius* may eventually prove to be a junior synonym of *Uintornis.* Because the Early Eocene genera *Sandcoleus* and *Anneavis* apparently have their closest affinities with the Middle Eocene genus *Eobucco,* rather than the contemporary genus *Chascacocolius,* it seems equally plausible that *Uintornis* may be a Middle Eocene relative of *Chascacocolius,* although such a relationship is not implied here.

In its postcranial skeleton, this species is the most coly-like of the Sandcoleiformes yet known. The narrow bill and extremely large retroarticular process of the mandible suggest that it was highly specialized for foraging by gaping, unlike the Coliidae (Fig. 4). Similar adaptations are widespread among the Passeriformes, especially in the Sturnidae, Icterinae, and Drepanidini. Gaping adaptations have evolved within each of these groups and of themselves are not diagnostic at any taxonomic level above the genus. By contrast, gaping adaptations are rare in non-passerine birds, occurring only in the Upupidae, Phoeniculidae, Haematopodidae, and some Scolopacidae. *Chascacocolius* shows that primitive coly-like landbirds had already radiated into some passerine "niches" by the Early Eocene.

The holotype of this species was preserved in the same nodule as articulated partial skeletons of marsupials, primates, an insectivore and a lizard.

This species is smaller than other known members of the family.

MEASUREMENTS (mm) OF HOLOTYPE. Left and right, respectively, are given for paired elements when both are present.

Quadrate (Right). Length of otic process from intercondylar notch, 6.1; width of condyles of otic process, 3.7; width of mandibular condyles, 4.9.

Mandible. Minimum length, 35.6; length of internal process from lateral cotyla, —, 5.2; width of cotylae, —, 4.1; length of retroarticular process from internal process, —, 8.6; depth of mandible, —, 3.9.

Coracoid. Length, —, 17.8; width of sternal articulation, 7.0, 6.7; length of procoracoid, 1.9, 1.7; width of glenoid facet, 1.7, 1.8; width of midshaft, —, 1.6.

Scapula (Right). Length, >20; width of shaft, 1.9; width of glenoid facet, 1.7.

Humerus. Length, 26.5, 26.5; length of pectoral crest from caput, 12.2, 12.9; length of bicipital crest from caput, 6.5, 6.1; diameter of midshaft, 2.5, 2.5; distal width, 6.1, 6.3; depth of condyles, 3.4, 3.4.

Radius. Length, 23.8, —; proximal width, 2.5, —; diameter of midshaft, 1.4, 1.2; distal width, 2.9, 2.9.

Ulna (Right). Length, 26.3; maximum proximal width, 4.1; diameter of midshaft, 2.3; depth of dorsal condyle, 3.6.

Carpometacarpus (Left). Length, 15.9; width of trochlea, 2.8; length from alular process to extensor process, 2.7; height of extensor process from trochlea, 4.9; anteroposterior diameter of midshaft of major metacarpal, 1.3; intermetacarpal width, 1.4; width of articular facet for major digit, 2.3.

Pelvis. Length of synsacrum, 21.7; width of body of synsacrum, 5.0; estimated width across antitrochanters, 15.2; length of posterior ala of ilium from acetabulum, 17.7; length of ischium from acetabulum, 18.2.

Femur (Left). Length, 25.1; length of head from trochanteric crest, 5.1; diameter of head, 2.4; height of trochanteric crest, 3.4; diameter of midshaft, 2.1; distal width, 4.9; height of medial condyle, 2.7; height of lateral condyle and tibiofibular crest, 3.9.

Tibiotarsus (Right). Width of cnemial crest, 5.8; width of cotylae, 4.3; proximal depth (cnemial crests to cotylae), 4.5; distance from proximal articular surface to distal end of fibular crest, 11.6; height of fibular crest (diameter of shaft plus elevation of ridge), 3.9; maximum width of shaft, 2.5; distal width, 3.9.

Botauroides Shufeldt 1915

INCLUDED SPECIES. *Botauroides parvus* Shufeldt 1915, the type and only known species of this genus.

DIAGNOSIS. Not examined; see Feduccia and Martin (1976).

Botauroides parvus Shufeldt 1915

HOLOTYPE. YPM 1030, distal end of left tarsometatarsus.

DIAGNOSIS. Not examined; see Feduccia and Martin (1976).

TYPE LOCALITY. Spanish John Meadow, Wyoming.

TYPE HORIZON. Bridger Formation, Wyoming.

REFERRED SPECIMENS. None

COMMENTS. *Botauroides* was thought by Shufeldt (1915) to be a heron (Ardeidae), only to be transferred later by Feduccia and Martin (1976) to the Primobucconidae, the supposed relatives of puffbirds (Bucconidae). We cannot be certain that this genus is properly included in the Sandcoleidae, because we have not examined the only known specimen.

SYSTEMATIC COMPARISONS

This section surveys the major similarities between sandcoleiforms and a diversity of modern arboreal birds. Our purpose here is to justify the ordinal status of the Sandcoleiformes and to justify its placement somewhat near the Piciformes, but nearest to the Coliiformes.

When describing a new taxon, it is necessary only to make comparisons to existing taxa that belong to the next inclusive unit of categorical hierarchy, usually within a genus, family, or

order. Because we decribe the Sandcoleiformes as a new order, it is necessary to make comparisons with a wide variety of birds, representing many different orders. In the Description and Diagnosis sections of this paper, we limited comparisons to those taxa of extant birds that we believe are most similar in appearance to sandcoleiforms as a "best guide" to the recognition of sandcoleiform fossils. However, in this section we outline the similarities between sandcoleiforms and representatives of many orders to illustrate that they share some characters with a wide variety of arboreal birds.

We compared Sandcoleiformes with members of Olson's (1985) higher landbird assemblage, to which we believe the Sandcoleiformes belong, as well as some members of Olson's basal landbird assemblage. Based on our general knowledge of comparative avian anatomy, we believe that the relationships of the Sandcoleiformes do not lie among Olson's waterbird assemblage or among the terrestrial members of the basal landbird assemblage.

We did not summarize the comparisons in the form of a table or a cladogram because most shared characters differ qualitatively in as many ways as the number of different birds that possess them. Moreover, we are not presently confident of our ability to distinguish between primitive and derived states of characters in the Sandcoleiformes, given the relatively poor consensus on the interordinal relationships among the higher landbirds.

In the paragraphs that follow, the descriptions refer to the taxon named in each heading. Similarities always refer to characters of the taxon specified at the beginning of each paragraph, and they are comparative to characters of the Sandcoleiformes.

GLAREOLIDAE. This family is mentioned only because the osseous canal of the external ophthalmic vessels passes between the facets for the articulation with the quadrate, directly across the dorsal pneumatic recess, as in sandcoleiforms. The osseous canal in glareolids, however, is very small and is otherwise not similar in morphological details to the fossils.

FALCONIDAE. The only strong similarities of falcons to sandcoleids are the following: the zygomatic process is short, and the tympanic cavity is similar in its detailed structure, especially the osseous canal of the occipital ramus of the external ophthalmic vessels and the very large lateral orbitonasal foramen of the duct of the nasal gland. There is also a superficial similarity in the humerus because of its robustness, curvature, and flared pectoral crest and in the tarsometatarsus because it is flattened.

PSITTACIDAE. Similarities of parrots to sandcoleids are only superficial and include the following: the carpometacarpus has a blunt distal end; the femur is similar in proportions to that of the fossils, especially in the large head; the tarsometatarsus (Figs. 15, 16) is flattened and has widely spaced cotylae and a low intercotylar eminence; the hypotarsus has three canals (or two canals and one groove); and the trochleae are splayed.

MUSOPHAGIDAE. The most notable similarities of the touracos to sandcoleids are the following: the lateral orbitonasal foramen of the duct of the nasal gland is large and positioned laterally; the sternum has four notches in the posterior margin, a shallow carina, crossed coracoidal sulci, and a flat manubrium; and the pygostyle is large, with a broad ventral surface. Other similarities include the following: the zygomatic and postorbital processes are small; the mandibular symphysis is small; the cervical vertebrae have pneumatic foramina and sometimes an accessory osseous bridge that connects the transverse process with the posterior articular process to form a lateral accessory foramen; the coracoid has a large lateral angle; the humerus has a pronounced bicipital crest and a broad, shallow coracobrachial depression; the radius is short and has a large condyle; the ulna is short and has a short, rounded olecranon and large, rounded dorsal process; the carpometacarpus has a blunt distal end; and the tarsometatarsus has a large scar for the articulation of the hallux, is thin in the region of the medial proximal vascular canal, and has an elongated collateral flange of trochlea IV.

CUCULIDAE. Similarities of certain cuckoos (e.g., *Eudynamys*) to sandcoleids include the following: the mandibular symphysis is small; the bill is superficially similar in shape; the sternum has caudomedial trabeculae that converge toward the midline distally; the carpometacarpus has a blunt distal end, a wide intermetacarpal space, and no intermetacarpal process; the ulna is short, with a short, rounded olecranon; the radius has a large distal condyle; and the tarsometatarsus is flattened and has a large, strongly inflected collateral flange of trochlea IV.

STRIGIDAE AND TYTONIDAE. The only notable similarities of owls to sandcoleiforms are the following: the proximal three phalanges of digit IV of the pes are extremely reduced in length, with the relief of the interphalangeal articular surfaces (i.e., notch and groove) being much exaggerated. As in the Falconidae, the osseous canal of the external ophthalmic vessels is large and passes between the facets for articulation with the quadrate, but in owls this is connected to the pila prootica rather than passing directly across the dorsal pneumatic recess. In owls, the sternum has four notches in the posterior margin (except *Tyto* Billberg 1828), the carpometacarpus has a blunt distal end, and the tarsometatarsus is flat and concave posteriorly, but these elements are otherwise not morphologically similar to those of sandcoleids.

CAPRIMULGIDAE, PODARGIDAE, NYCTIBIIDAE, AND STEATORNITHIDAE. These share no important similarities with sandcoleids except that the cervical vertebrae of *Podargus* have an accessory process connecting the transverse and posterior articular processes and the pygostyle is superficially similar.

AEGOTHELIDAE. Similarities of owlet-frogmouths to sandcoleids include the following: the sternum in general, particularly the pattern of the sternal notches, and the ischium and ilium have long terminal processes. Other interesting similarities include the following: the skull, which has less pneumatization than in other caprimulgiform families, has a small zygomatic process; the cervical vertebrae have pneumatic foramina; the humerus, similar in its curvature and robustness to the fossils, with a pronounced bicipital crest, and a well-rounded radial condyle; the femur with a tubercle (although small) for the attachment of m. gastrocnemius lateralis and ansa m. iliofibularis; and the pygostyle in general.

APODIDAE. The most notable similarities of swifts to sandcoleids are the following: the proximal three phalanges of digit IV of the pes are extremely reduced in length, and the terminal phalanges of the pes are large. Other similarities are the following: the carpometacarpus has a blunt distal end; the tibiotarsus has a crest opposite the fibular crest; and the tarsometatarsus is flattened, has widely spaced cotylae, a low intercotylar eminence, and a concave plantar surface.

COLIIDAE. Of all families of modern birds, the colies are the most similar to sandcoleids in general proportions as well as in morphological details, especially of the humerus and hindlimb (see Figs. 8, 9, 12–17, Diagnosis of the Sandcoleiformes, and Description of the Sandcoleidae). Yet, significant differences exist between colies and sandcoleids, in which the latter are more like other families described in this section. The *differences* of colies include the following: the bill is short; the tympanic cavity does not have the large canal of the external ophthalmic vessels passing centrally across the dorsal pneumatic recess; the

quadrate and zygomatic process have flattened lateral surfaces; the quadrate has a process projecting dorsad from the lateral mandibular condyle; the pterygoids are cylindrical; the sternum has a different pattern of sternal notches and a short sternocoracoid process; the furcula has a hypocleideum; the scapula has a process for the articulation of the furcula; the carpometacarpus has a well-developed intermetacarpal process; the pelvis has neither a large ischiopubic fenestra nor a broad terminal process of the ischium; and the pygostyle has Picidae-like transverse processes.

TROGONIDAE. Similarities of the trogons to sandcoleids are superficial and include the following: the sternum has four notches in the posterior margin; the scapula does not have a large process for the articulation of the furcula; the proportions of forelimb elements; the humerus has a long pectoral crest, a pronounced, narrow bicipital crest, and a broad, shallow coracobrachial region; and the carpometacarpus has a blunt distal end (Fig. 18).

ALCEDINIDAE, TODIDAE, MOMOTIDAE, MEROPIDAE, AND CORACIIDAE. Similarities to sandcoleiforms are few, but include the following: the sternum with four notches in the posterior margin; the furcula has no hypocleideum; and the coracoids of todids and coraciids have combinations of characters such as the well-developed medial angle, lateral process, narrow shaft, small procoracoid (not Coraciidae), and a small scapular extremity.

LEPTOSOMIDAE. In addition to the few similarities for other families of Coraciiformes listed earlier, cuckoo-rollers are similar to the fossils because of the following: in the tympanic cavity, the osseous canal of the external ophthalmic vessels passes between the facets for the articulation with the quadrate and the lateral facet is nestled into the zygomatic process; some cervical vertebrae have an accessory process connecting the transverse process and posterior articular process; the scapula is without a large articular process for the furcula; the humerus has a long, flared pectoral crest that comes to an angle approximately at midlength of the crest; the tarsometatarsus is broad and has widely spaced cotylae, a low intercotylar eminence, and a flattened shaft; and the collateral flange of trochlea IV is exaggerated posteriorly.

UPUPIDAE AND PHOENICULIDAE. Hoopoes and woodhoopoes exhibit only a few similarities to the fossils, including the following: the mandible with a long retroarticular process (among sandcoleids, only *Chascacocolius* new genus, described previously, is known to have an elongated retroarticular); the cervical vertebrae have an accessory process connecting the transverse and posterior articular process; the carpometacarpus has a blunt distal end; and the ischiopubic fenestra is large.

GALBULIDAE. The only similarities of jacamars to sandcoleids are the following: the zygomatic process is small; the cervical vertebrae have pneumatic foramina and an accessory process connecting the transverse and posterior articular processes; the sternum has four notches in the posterior margin (although the pattern is like that of coliids, not like sandcoleids); the tarsometatarsus is short and flattened; and the pygostyle is generally similar.

BUCCONIDAE. The only similarities of puffbirds to sandcoleids are the following: the cervical vertebrae have accessory processes connecting the transverse and posterior articular processes; the scapula has no large articular process for attachment of the scapula; and the sternum has four notches in the posterior margin (although the pattern is like galbulids and coliids, not like sandcoleids) (see Figs. 15, 16).

CAPITONIDAE. Similarities of barbets to sandcoleids are restricted to the following: the sternum because of the configuration of the caudal trabeculae (e.g., *Calorhamphus* Lesson 1839, *Gymnobucco* Bonaparte 1850, and *Lybius* Hermann 1783); the furcula has no hypocleideum; the tibiotarsus has a broad cnemial region (intercristal sulcus; e.g., *Trachyphonus* Ranzani 1821, not *Tricholaema* Verreaux and Verreaux 1855); and the ischium has a long, bent terminal process (e.g., *Tricholaema*).

INDICATORIDAE. Among the Pici, the honeyguides are the most similar to the fossils because of the following: the cranium is well rounded; the supraorbital region is narrow; the frontal bones diverge anteriorly and are not incised by the prefrontals; the lateral orbitonasal foramen is large and positioned very laterally; the zygomatic process is small; the pterygoid has ridges along its entire length; the mandibular symphysis is small; the cervical vertebrae have pneumatic foramina; the pygostyle has no transverse processes; the sternum (Fig. 6) is similar in general, except that the spina externa of the manubrium (which is bifid in *Prodotiscus* Sundevall 1850, unlike the fossils) forms a continuous ridge with the procumbent anterior margin of the carina; the furcula has no hypocleideum; the coracoid is narrow, although narrower than in sandcoleids; the pelvis is similar in all details, especially the large obturator and ilioischiadic foramina and the large ischiopubic fenestra with a long, bent terminal ischial process; and the tibiotarsus as in the Capitonidae.

RAMPHASTIDAE. The only similarities of toucans to sandcoleids are the following: the lateral orbitonasal foramen is positioned laterally in *Baillornis* Cassin 1867, *Selenidera* Gould 1837, and *Aulacorhynchus* Gould 1834, and the cervical vertebrae with pneumatic foramina.

JYNGIDAE. Wrynecks are almost as similar to the fossils as are the indicatorids. Typically of the Pici, similarities include the following: the sternum because of the morphology of the sternal notches; the tibiotarsus in general; and the ischium with a long, bent terminal process (Fig. 11).

PICIDAE. Similarities of the diverse woodpecker family to sandcoleids include the following: the orbitonasal foramen is positioned laterally; the cervical vertebrae have an accessory process connecting the transverse and posterior articular processes (e.g., *Picus* Linnaeus 1758); the sternum has a shallow carina and a configuration of the caudal trabeculae similar to that of the fossils; the furcula has no hypocleideum; the humerus has a well-developed lateral epicondyle and bulbous capitulum; the pelvis has a large ischiopubic fenestra and a long, bent terminal process of the ischium (especially *Picus*), although shorter than in sandcoleids; the femur has a tubercle for the attachment of m. gastrocnemius lateralis and ansa iliofibularis, although small; the tibiotarsus because of the configuration of the cnemial crests (although they are more symmetrical in anterior view than in sandcoleids) and a crest opposite the fibular crest (Fig. 13).

PASSERIFORMES. Similarities of perching birds to sandcoleiformes are rare and include the following: a skull that is well rounded in some species; a long retroarticular process of mandible in some (e.g., *Sturnella* Vieillot 1816 and *Sturnus* Linnaeus 1758); a sternum with four notches in the posterior margin (i.e., some scytalopodids); a pelvis with a large ischiopubic fenestra and long terminal process of the ischium (e.g., *Ampelion* Tschudi 1845); and the tibiotarsus with a crest on the tibiotarsus opposite the fibular crest.

DISCUSSION

The order Sandcoleiformes represents an archaic group with no close relationships among modern birds. Most similarities are

with the Coliidae, but there are also very close similarities to the Pici, particularly the Indicatoridae. Even among more disparate orders of landbirds, there are families or genera that share similarities with sandcoleids that the coliids and Pici do not. Such characters are likely primitive, if not evolved convergently. This suggests a very early origin and divergence of the Sandcoleiformes from all known orders of birds. Sibley et al. (1988) suggested that the Pici are the sister-group of Coliidae plus other higher landbirds. If this were so, then the strong similarities of Sandcoleiformes to the Coliidae and Pici and weaker similarities to other groups could indeed be shared primitive characters, retained since the early divergence of the lineages leading to the Pici, Coliiformes, Sandcoleiformes, and other higher landbirds.

The ecology of Sandcoleiformes, like most birds, is best reflected by the specializations of their bills and feet. The bill of *Sandcoleus* is similar in overall proportions to that of *Eudynamys* or *Turdus*. *Sandcoleus* could have been a generalist, eating anything from berries, fruits, and seeds to hard- and soft-bodied invertebrates. The bill of *Chascacocolius* is perhaps as specialized as that of any living bird for gaping as a mode of foraging. Gaping in landbirds is typically associated with an insectivorous diet, and modern gapers may forage either on the ground or in trees.

All sandcoleiformes appear to have been both facultatively zygodactyl and pamprodactyl. We believe that, like all zygodactyl or facultatively zygodactyl birds, sandcoleiforms could oppose digit IV to digits II and III. This is because trochlea IV of the tarsometatarsus is relatively narrow and the lateral flange is very large and extends caudad or caudomediad in the manner of a sehnenhalter. Moreover, there is a large distal foramen, and to varying degrees there is a groove medial to trochlea IV on the anterior aspect of the shaft.

In their description of the hindlimb myology of the Coliidae, Berman and Raikow (1982) could identify only a few myological traits that might be directly associated with pamprodactyly; however, because they did not specifically discuss or illustrate any of the muscular origins and insertions on the pelvic skeleton itself, we could not ascertain whether or not any of these adaptations are present in the Sandcoleidae. Sandcoleiforms possess particularly large processes and ridges for the origins and insertions of the distal musculature of the pelvic appendage and in general closely resemble colies in these respects. Moreover, the coly-like location of the large facet for the articulation of metatarsal I on the medial surface of the tarsometatarsus, rather than on the plantar surface, would facilitate rotation of digit I mediad and anteriad. The most significant difference in the condition of the feet between the Coliidae and Sandcoleidae is that in the Coliidae the facet for metatarsal I is positioned more distad on the tarsometatarsus, and the tarsometatarsal trochleae are more closely spaced and none are significantly elevated proximad above the others. Although the Sandcoleidae possessed feet superficially similar to those of raptorial birds, they were probably not similarly adapted behaviorally. The bill of *Sandcoleus* was too weak to have been used efficiently in predation on anything other than small invertebrates, and the bill of *Chascacocolius* clearly indicates that its mode of food-fathering was bill-oriented rather than foot-oriented. The foot of sandcoleiforms was therefore probably specialized for climbing and creeping in trees.

The long rectrices of sandcoleids had somewhat thickened shafts, but no more so than those of colies or the more long-tailed species of parrots. The pygostyles of sandcoleiforms lack the specializations of the transverse processes that anchor the retrices in most species of Pici and Coliidae. Hence, the tails of sandcoleiforms would not have been structurally equivalent to those in these modern taxa.

One could imagine that the flight of sandcoleiforms might have been somewhat like that of species of the Pici or Coliidae. They were probably strong fliers, but they appear to have been poorly adapted for long periods of flight, because their wing was short and rounded and the carina of their sternum was shallow.

The order Sandcoleiformes is morphologically diverse and was probably much more speciose than is apparent from the relatively few fossil forms described here. Sandcoleiforms were probably numerically abundant as well, because they represent one of the two most commonly preserved orders of landbirds in the Lower Eocene of Wyoming (the other being the Lithornithiformes). Sandcoleiforms probably filled many of the niches similar to those later occupied by passerines. Replacement by modern orders of archaic early Tertiary groups, with no close living relatives, is a pattern also observed among mammals (Russell, 1982), where creodonts and condylarths, for example, were replaced by carnivores and ungulates.

Sandcoleiforms fit another pattern that is becoming increasingly familiar in avian paleontology: the occurrence of groups in North America whose closest living relatives are now geographically distant and often insular. Colies, if they are the nearest relatives of sandcoleiforms, are restricted to Africa, although their range once extended as far north as France (Mourer-Chauviré, 1982). Sandcoleiformes appear to fulfill Olson's (1985) prophecy of the discovery of coly-like birds elsewhere in the Tertiary outside of Africa. The closest similarities to Lithornithiformes are among the tinamous (Tinamidae) of Central and South America and the kiwis (Apterygidae) of New Zealand (Houde, 1988). Olson (1987) recently identified a primitive relative of the South American oilbird (Steatornithidae), and Houde and Olson (1989) identified fossils similar to the Madagascan ground-rollers (Atelornithidae), both from the Lower Eocene of Wyoming.

The known fossil record of the Sandcoleiformes is brief, lasting only from the Early to Middle Eocene. Although future discoveries may push their record back into the Paleocene, it appears unlikely that they persisted much after the Middle Eocene. No certain members of the Sandcoleiformes have been identified in the large avifaunas from the Middle Eocene excavations at Messel, Germany, and the Eo-Oligocene at Quercy, France. However, a single humerus (Paris Museum QU 17092) from an unknown level of the Phosphorites du Quercy that was designated the holotype of *Primocolius sigei* Mourer-Chauviré 1988 (Coliidae) is, in our opinion, more similar to *Chascacocolius* than it is to *Colius*, because the shaft is robust and curved, the medial epicondyle is short, the pectoral crest is large, and there is no bony spur in the tricipital fossa that is distinctive of colies. We have not had the opportunity to compare other specimens that were referred to *P. sigei*, which include a carpometacarpus in addition to humeri. An unpublished single tarsometatarsus (Basel Museum QO 596), also identified as a coly (C. Mourer-Chauviré, pers. comm.) and also from an unknown level of the Phosphorites du Quercy is intermediate between *Anneavis* and *Colius* with respect to its robustness and width, and splaying and elevation of trochleae II and IV.

The impracticality of identifying isolated elements from early Tertiary birds (Olson, 1977) is underscored by the discovery of this, yet another, group of birds with no close affinities to modern birds that combines a mosaic of characters similar to individual parts of various unrelated taxa of modern birds. The fact that *Uintornis* and *Botauroides* had been assigned to no fewer

than four families of modern birds attests to the riskiness of this practice. Harrison (1980:83) described "a small owl from the Lower Eocene of Britain," on the basis of a single proximal pedal phalanx of digit III. The specimen, he declared, "is sufficiently specialized to be recognised as that of an owl." Specifically, it is short and the distal articular surface extends onto the dorsal aspect of the bone. While we do not suggest that *Eostrix vincenti* Harrison 1980 is actually a member of the Sandcoleiformes, we do point out that much of the same condition of the pedal phalanges occurs in Sandcoleiformes as well as in Strigiformes and other groups.

Hoch (1975:552, fig. 6) referred a small humerus (Mineralogical Museum of Copenhagen specimen MNH. V.P. 1282) from the lowermost Eocene of the Mo Clay to the Falconiformes but wisely did not name the specimen. This humerus is sufficiently dissimilar from humeri of the Falconiformes and similar to humeri of the known Sandcoleiformes that it might be correctly included in the latter. It has a large, broad pectoral crest, a narrow bicipital crest, and proportions similar to those exhibited by *Sandcoleus*. It is not a member of any genus for which the humerus is known, however, and its inclusion in the Sandcoleiformes is unwarranted at this time.

SUMMARY AND CONCLUSIONS

The order Sandcoleiformes includes one family with seven species in six genera. The monotypic genera *Sandcoleus*, *Anneavis*, and *Chascacocolius* are described as new, with the previously described genera *Eobucco*, *Unitornis*, and *Botauroides* being referred to the family. The known distribution of the Sandcoleiformes is limited to Lower and Middle Eocene deposits of Wyoming.

The order Sandcoleiformes is not phylogenetically close to any other known order of birds; still, it may be closer to the order Coliiformes than it is to any other. Sandcoleiforms resemble colies postcranially, and, to a lesser degree, they also resemble members of the Pici and other groups. At least some had short remiges and long, tapered rectrices, like those of colies. However, sandcoleiforms were more diverse than known colies, because they were specialized for at least two very different modes of feeding. Some possessed a thrush-like bill, whereas one had a gaping bill like that of certain icterids. Thus, sandcoleiforms may have occupied niches that are currently exploited by passerines.

ADDENDUM

Plates I and II were not completed in time to be included in the text references in this paper. They were intended to replace several of the figures called out in the text and are presented to augment those figures.

Plate I. *Sandcoleus copiosus*, holotype specimen (USNM 433912): **a,** skull, ventral view; **b,** right quadrate, lateral view; **c,** cervical vertebra, right lateral view; **d,** right posterior portion of mandible, dorsal view; **e,** pelvis, dorsolateral view; **f,** right coracoid, ventral view; **g,** left coracoid, ventral view; **h,** right coracoid, dorsal view; **i,** left coracoid, dorsal view; **j,** pygostyle, right lateral view; **k,** skull, dorsolateral view; **l,** left posterior portion of mandible, dorsal view; **m,** pelvis, ventral view; **n,** sternum, ventral view; **o,** sternum, left lateral view; **p,** left and right scapulae, lateral and medial views, respectively; **q,** right humerus, cranial view; **r,** left humerus, cranial view; **s,** right humerus, caudal view; **t,** left humerus, caudal view; **u,** right ulna, caudal view; **v,** left ulna, caudal view; **w,** right ulna, cranial view; **x,** left ulna, cranial view; **y,** right radius, cranial view; **z,** left radius, cranial view; **aa,** right radius, caudal view; **bb,** left radius, caudal view; **cc,** left carpometacarpus, dorsal view; **dd,** left carpometacarpus, ventral view; **ee,** right femur, cranial view; **ff,** right femur, caudal view; **gg,** left femur, cranial view; **hh,** left femur, caudal view; **ii,** right tibiotarsus, cranial view; **jj,** left tibiotarsus, cranial view; **kk,** right tibiotarsus, caudal view; **ll,** left tibiotarsus, caudal view; **mm,** right tarsometatarsus, dorsal view; **nn,** right tarsometatarsus, plantar view; all approximately actual size; all treated with ammonium chloride.

Plate II. *Chascacocolius oscitans*, holotype specimen (USNM 433913), top two rows (a–w); *Colius striatus* (USNM 558544), third and fourth rows (aa–uu); and *Trogon viridus* (USNM 562749), bottom row (aaa–fff): **a,** symphysis and right posterior portion of mandible; **b,** furcula, cranial view; **c,** right coracoid, ventral view; **d,** left coracoid, ventral view; **e,** right coracoid, dorsal view; **f,** left coracoid, dorsal view; **g,** right scapula, lateral view; **h,** right humerus, cranial view; **i,** left humerus, cranial view; **j,** right humerus, caudal view; **k,** left humerus, caudal view; **l,** left innominate, lateral view; **m,** right ulna, caudal view; **n,** right ulna, cranial view; **o,** distal portion of right radius, cranial view; **p,** left radius, cranial view; **q,** left radius, caudal view; **r,** left carpometacarpus, dorsal view; **s,** left carpometacarpus, ventral view; **t,** left femur, cranial view; **u,** left femur, caudal view; **v,** proximal and distal portions of right tibiotarsus, cranial view; **w,** proximal portion of right tibiotarsus, caudal view; **aa,** right coracoid, ventral view; **bb,** right coracoid, dorsal view; **cc,** right humerus, cranial view; **dd,** left humerus, cranial view; **ee,** right humerus, caudal view; **ff,** left humerus, caudal view; **gg,** right ulna, caudal view; **hh,** right ulna, cranial view; **ii,** right radius, cranial view; **jj,** right radius, caudal view; **kk,** left carpometacarpus, dorsal view; **ll,** left carpometacarpus, ventral view; **mm,** right quadrate, lateral view; arrow indicates dorsal process of lateral mandibular condyle; **nn,** left femur, cranial view; **oo,** left femur, caudal view; **pp,** right tibiotarsus, cranial view; **qq,** left tibiotarsus, cranial view; **rr,** right tibiotarsus, caudal view; **ss,** left tibiotarsus, caudal view; **tt,** right tarsometatarsus, dorsal view; **uu,** right tarsometatarsus, plantar view; **aaa,** right humerus, cranial view; **bbb,** right humerus, caudal view; **ccc,** right coracoid, ventral view; **ddd,** right coracoid, dorsal view; **eee,** left carpometacarpus, dorsal view; **fff,** left carpometacarpus, ventral view; all approximately actual size; a–w treated with ammonium chloride.

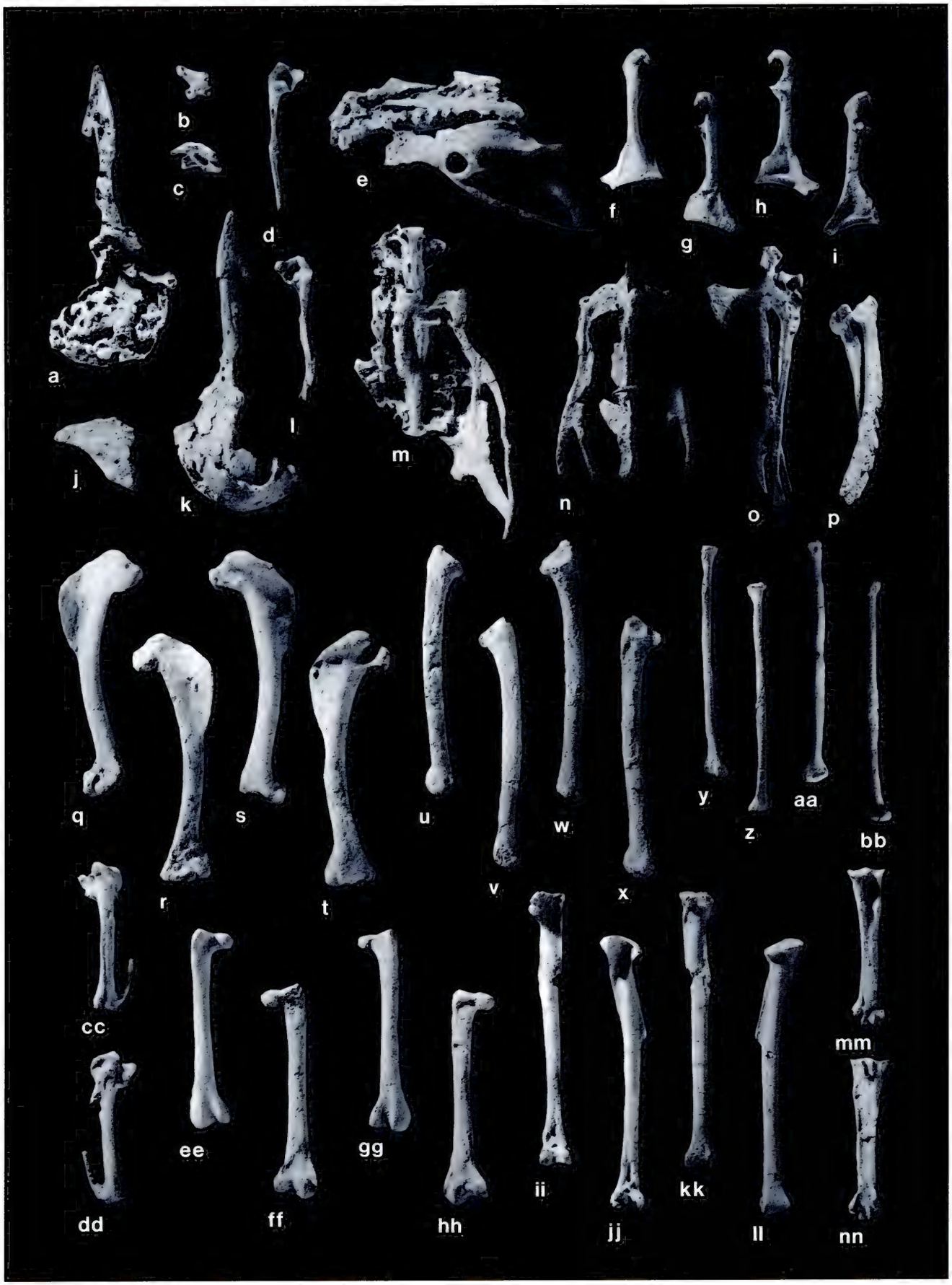
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Plate I

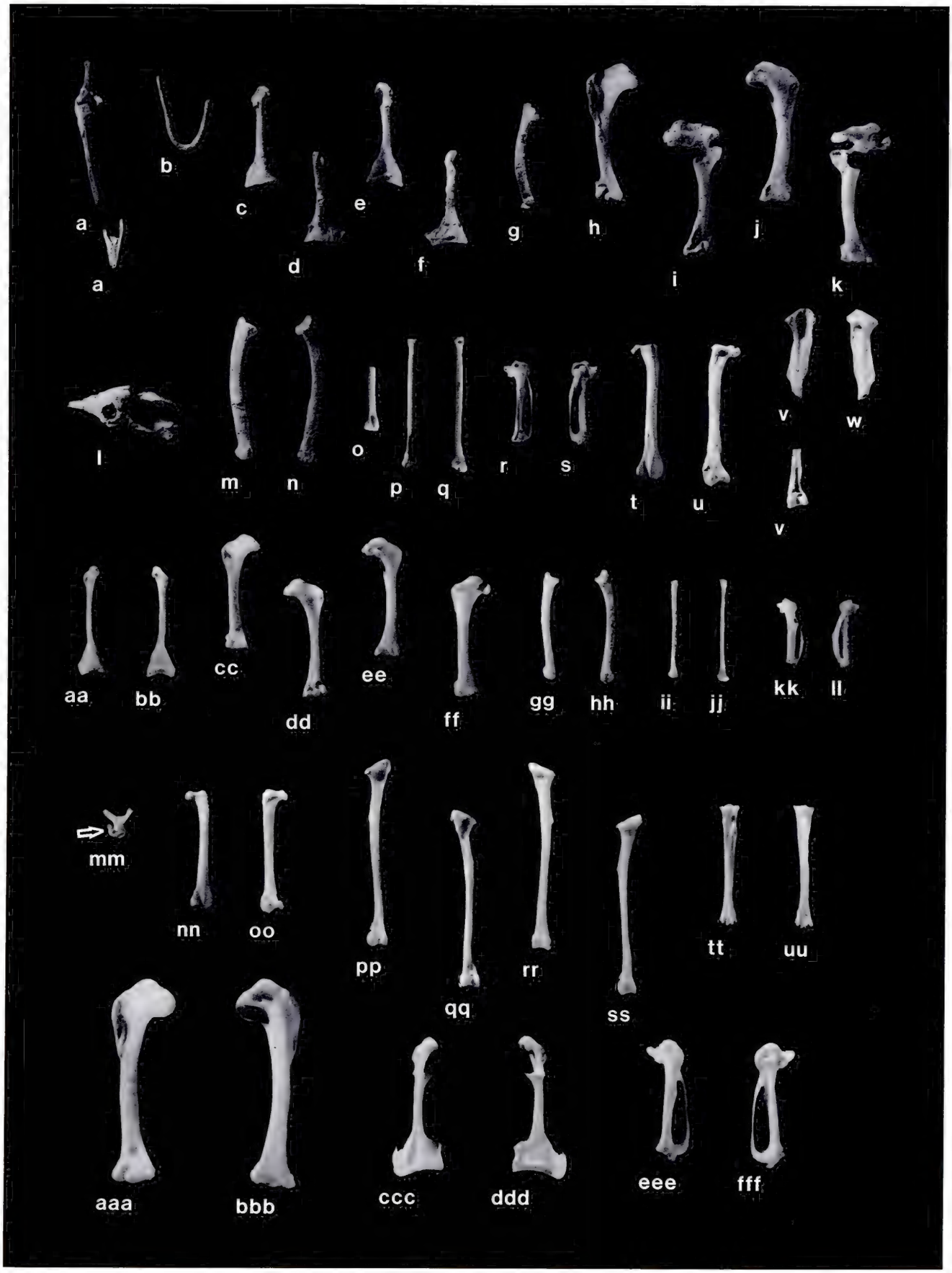
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Plate II

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A NEW SPECIES OF OWL (AVES: STRIGIFORMES) FROM THE MIDDLE EOCENE MESSEL OIL SHALE

Dieter Stefan Peters

ABSTRACT. The postcranial skeleton of a small owl from the oil shale of Messel (Middle Eocene, Lower Geiseltalium) is described as *Palaeoglaux artophoron* new species. The family Palaeoglaucidae Mourer-Chauviré 1987 is different from all other known families of owls, but it is not possible to determine the phylogenetic relationships of the paleoglaucids because the phylogeny of owls is so poorly known. The unusual plumage structure of *P. artophoron* and its possible significance is discussed.

ZUSAMMENFASSUNG. Das postcraniale Skelett von *Palaeoglaux artophoron* n. sp., einer kleinen Eule aus dem Ölschiefer von Messel (Mittel-Eozän, Unteres Geiseltalium), wird beschrieben und mit anderen fossilen und rezenten Eulen verglichen. Die Familie Palaeoglaucidae Mourer-Chauviré 1987 weicht von allen anderen Eulen ab. Ihre genealogischen Beziehungen lassen sich zur Zeit kaum rekonstruieren, da die Phylogenie der Eulen insgesamt nur unzureichend bekannt ist. Das ungewöhnliche Gefieder von *P. artophoron* und seine mögliche Bedeutung werden kurz diskutiert.

Key words: Aves, Strigiformes, *Palaeoglaux*, Palaeoglaucidae, phylogeny, plumage, Eocene, Messel.

INTRODUCTION

The fossil record of owls begins in the Paleocene, with *Ogygoptynx* Rich and Bohaska 1981 from Colorado and *Sophiornis* Mourer-Chauviré 1987 from France. During the Eocene, at the latest, owls underwent a considerable radiation, with no less than 2 families comprising 7 genera and 11 species being described from the Phosphorites du Quercy, France, alone (Mourer-Chauviré, 1987). Additional species of Eocene owls are known from Europe and North America, although the fossil record of most species is based on only scarce, fragmentary remains. The specimen discussed herein is the first articulated skeleton of an Eocene owl to be described.

Many fossil birds have been found in the lake deposits of Grube Messel (Peters, 1988), but among these raptorial species are quite rare. Only two specimens of the order Falconiformes are known, and the specimen described herein is the only owl ever recovered from the site. It may be that raptors of the time were predominately forest birds, thereby avoiding the trap-effect of the lake (Franzen, 1985), or that they were simply still uncommon birds. General information about the Messel site was given by Hoch (1980) and Franzen (1985); for more details see Schaal and Ziegler (1988).

MATERIALS

Comparative specimens were examined from the following extant species of owls: *Phodilus badius* (Horsfield 1821), *Tyto alba alba* (Scopoli 1769), *T. a. guttata* (C.L. Brehm 1831), *T. a. glaucops* (Kaup 1852), *Otus asio* (Linnaeus 1758), *Otus bakkamoena* Pennant 1769, *Bubo bubo* (Linnaeus 1758), *Buto virginianus* (Gmelin 1788), *Nyctea scandiaca* (Linnaeus 1758), *Pulsatrix perspicillata* (Latham 1790), *Glaucidium brasilianum* (Gmelin 1788), *Glaucidium passerinum* (Linnaeus 1758), *Ninox novaeseelandiae* (Gmelin 1788), *Athene noctua* (Pontoppidan 1763), *Speotyto cunicularia* (Molina 1782), *Strix aluco* Linnaeus 1758, *Asio otus* (Linnaeus 1758), *Asio flammeus* (Pontoppidan 1763), and *Aegolius acadicus* (Gmelin 1788).

SYSTEMATICS

Order Strigiformes (Wagler 1830)

Family Palaeoglaucidae Mourer-Chauviré 1987 (n. stat.)

TYPE GENUS. *Palaeoglaux* Mourer-Chauviré 1987.

EMENDED DIAGNOSIS. Coracoideum pneumatic, with elevation of processus acrocoracoideus overhanging sulcus m. supracoracoidei; humerus with sulcus ligamentosus transversus extending proximad to tuberculum ventrale; ulna with proximal end dorsoventrally rather narrow; radius without ossified arch; tarsometatarsus resembles that in *Necrobyas* Milne-Edwards 1892, but with shaft more slender, transition between fossa m. flexoris hallucis brevis and sulcus flexorius lower, and plantar wing of trochlea metatarsi II shorter; distal tarsal phalanges with tuberculum flexorium comparatively long proximodistally and in plantar view nearly dumbbell-shaped.

Genus *Palaeoglaux* Mourer-Chauviré 1987

TYPE SPECIES. *Palaeoglaux perrierensis* Mourer-Chauviré 1987.

DIAGNOSIS. As for family.

DESCRIPTION. The new species from Messel is in agreement with *Palaeoglaux* inasmuch as it has the tarsometatarsus with shaft expanded only a very little distally; trochlea metatarsi II with plantar wing comparatively short; coracoideum pneu-

Figure 1. *Palaeoglaux artophoron* n. sp. Holotype, SMF-ME 1144A, main slab. Coated with ammonium chloride. **1,** Dorsal end of left clavicle; **2,** left scapula; **3,** left manus; **4,** right fibula. 1.29×.

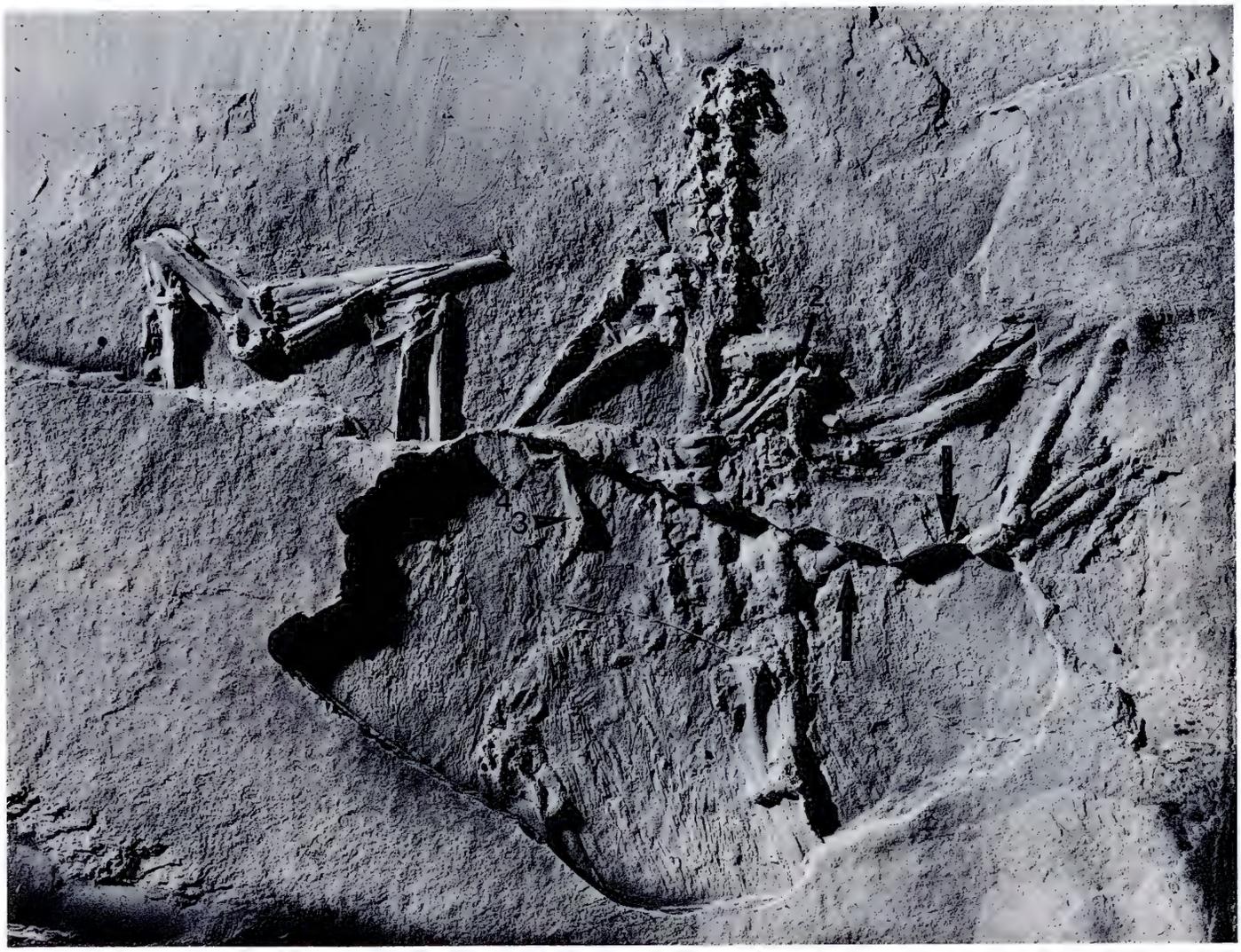

Figure 2. *Palaeoglaux artophoron* n. sp. Holotype, SMF-ME 1144B, counter-slab. Coated with ammonium chloride. During preparation (resin transfer method) the caudal part of the slab was erroneously displaced to the left compared with the cranial part. In the natural position, the big arrows should be facing each other. **1,** Right coracoideum; **2,** left coracoideum; **3,** crista sterni, cranial margin; **4,** furcula, symphysis. 1.44×.

matic; and ulna with proximal end appearing rather narrow dorsoventrally.

Palaeoglaux artophoron new species

Figures 1–8

HOLOTYPE. Slab and counter-slab with a nearly complete postcranial skeleton, Forschungsinstitut Senckenberg No. SMF-ME 1144, A, B.

DIAGNOSIS. Distinctly smaller than *Palaeoglaux perrierensis,* the only other known species of the genus.

TYPE LOCALITY. Ölschiefergrube Messel, Hessen, Germany.

TYPE STRATUM. Lower Middle Eocene, Lower Geiseltalium, Messel Formation.

ETYMOLOGY. Greek, *artophoron,* bread-basket; noun used in apposition; dedicated respectfully to Pierce Brodkorb.

DESCRIPTION. The anatomical terminology used herein is after Baumel et al. (1979), and the measurements (mm) follow those of Driesch (1976), unless otherwise indicated. Many of the measurements are estimates because all of the bones are fixed in the slabs, and most of them are more or less deformed.

Vertebrae. Only six cervical vertebrae are sufficiently preserved to permit study. Although the vertebrae fall within the morphological spectrum of strigiform cervicals, the specific and individual variation of vertebrae in owls does not permit the unequivocal identification of the fossil vertebrae to number. I consider the six cervicals tentatively as cervicals VI–XI, the alternative sequence V–X being less probable. The ventral surface of the corpora of cervicals VI–IX is flattened and cranially slightly concave, whereas in cervicals X and XI it forms a longitudinal crest with, in cervical XI, a ventral spine. The processus spinosus can be seen in cervicals VII–XI as low, blunt crests. The processus articulares caudales bear processus dorsales that are narrow and prominent in cervicals VI–VIII, but broader and less prominent in cervicals IX–XI. Measurements: Cervical VIII: medial length of lamina dorsalis arcus, 1.7; maximum breadth between lateral margins of processus articulares caudales, 6; length between cranial margin of corpus VI and caudal margin of corpus XI, 21.

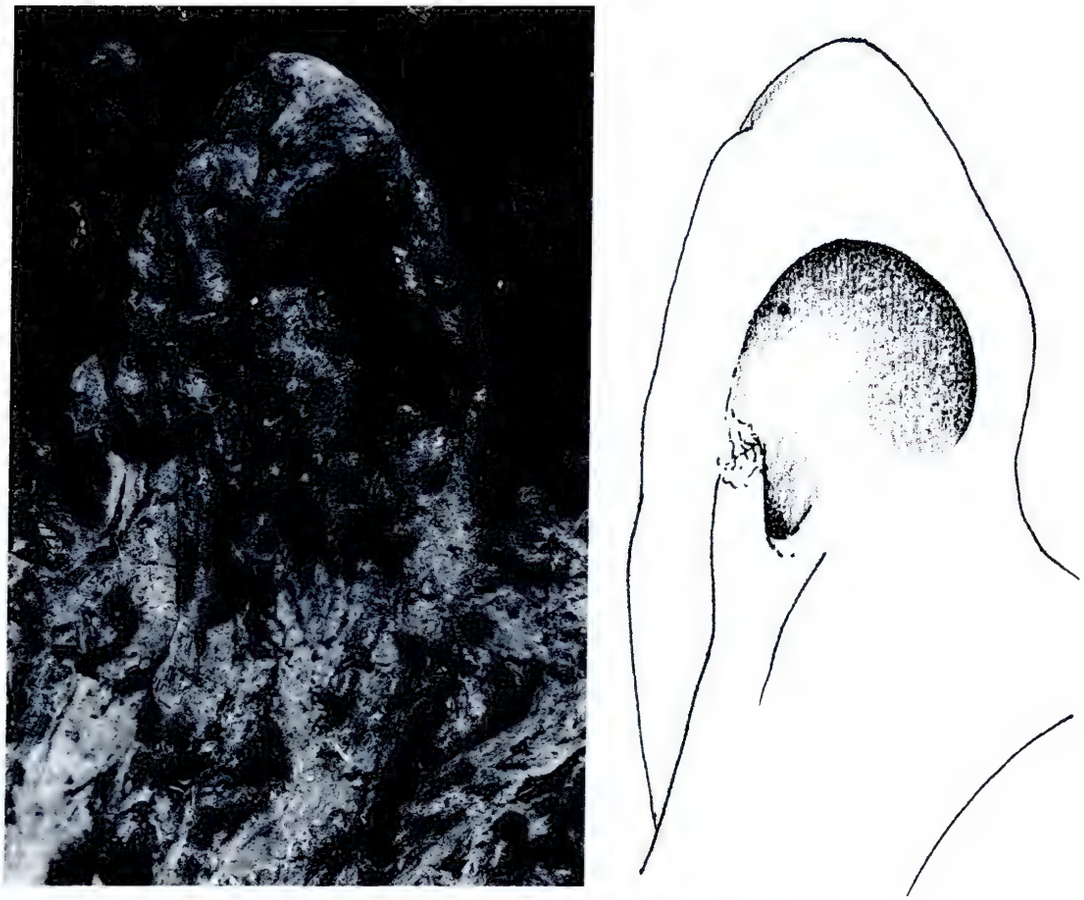

Figure 3. *Palaeoglaux artophoron* n. sp. Right coracoideum, extremitas omalis, medial view. 12.0×.

Sternum. The cranial margin of the crista sterni is preserved on the counter-slab (Fig. 2). It displays on its dorsal part two weak, rounded cristae laterales and between them a shallow sulcus divided longitudinally by a small, narrow crista mediana. The rostrum sterni and apex carinae are worn, but the remains of the apex suggest a closer similarity to the Strigidae than to the Tytonidae. Bony remnants can be seen on the main slab that might be parts of the right processus craniolateralis, but they are too fragmentary to yield any relevant information.

Furcula. The expanded dorsal end of the left clavicle and the fused sternal ends of both clavicles are preserved (Figs. 1, 2). The synostosis is drawn out into a small knob-like apophysis. The extremitas omalis is truncated at the end, approaching the condition in *Tyto* Billberg 1828. The lateral side is hidden from view so it is not known if the clavicles were pneumatic. Measurements: diameter of synostosis, including apophysis, 1; apical breadth of extremitas omalis, 3.8.

Scapula. Only parts of the left scapula are preserved (Fig. 1), and they are not particularly diagnostic. The elliptical facies articularis humeralis has a craniocaudal diameter of 3 mm and a dorsoventral diameter of 2 mm.

Coracoideum. The medial aspect of both coracoidea is exposed on the counter-slab (Fig. 2). Both coracoidea are badly crushed and both extremitates sternales are lacking, but the extremitas omalis of the right coracoideum is sufficiently preserved to reveal some important details (Fig. 3): The collum acrocoracoidei is comparatively short; an elevation of the processus acrocoracoideus overhangs the sulcus m. supracoracoidei ventrally and cranially; and a small foramen pneumaticum can be seen on one of the bony fragments of the sulcus, but more foramina may have existed. The proportions of the fragmentary shaft and procoracoid are similar to the general strigiform condition, but no further distinctions can be made. Measurements: maximum length (estimated), 18–19 mm.

Humerus. The humeri are wholly preserved, but they are badly crushed and only a few details are recognizable. The tuberculum dorsale is relatively strong, whereas the intumescentia and bicipital crest seem to be rather small. The distal ends are only moderately expanded. Although the proximal ends are too badly crushed to reveal details, the fragments suggest that the sulcus ligamentosus transversus extended proximal to the tuberculum ventrale, similar to the configuration found in the Strigidae. This would coincide with the fact that the foramen pneumaticum cannot be seen, because in strigid owls, and also in *Phodilus* Geoffroy Saint-Hilaire 1830, this foramen is greatly hidden by overhanging bone in ventral view and can easily be covered by fragments if the bone is crushed. The margo caudalis seems to be more pronounced than in all known owls. Measurements: maximum length of right humerus, 43; the left humerus seems to be much shorter (36) (the observed difference is certainly a result of the different distortions of the humeri; the estimated true length is 40); proximal breadth, 9.

Ulna. Both ends of the ulna are crushed or hidden from view, but most of the shaft can be seen. It is not very diagnostic,

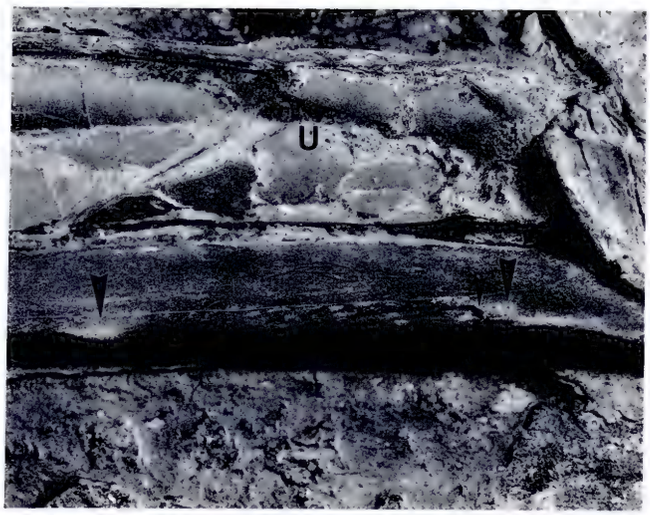

Figure 4. *Palaeoglaux artophoron* n. sp. Radius, section of the shaft. Big marks indicate points of attachment of the supposed connective tissue arch. Small mark indicates nutrient foramen. **U,** ulna. 8.45×.

Figure 5. *Palaeoglaux artophoron* n. sp. Right carpometacarpus, proximal end. **1,** Processus extensorius; **2,** digitus alulae, proximal phalange; **3,** doubtful ossicle (phalanx distalis alulae or os prominens?). 6.58×.

however. It appears that the proximal end was only slightly dorsoventrally expanded. Measurements: maximum length (estimated), 49.

Radius. The most interesting feature of this bone can be seen on the counter-slab, where the caudal aspect of the right radius is exposed (Figs. 2, 4). The osseous arch, present in most modern owls, is lacking. Nevertheless, there are two small elevations about 5 mm apart, with slightly roughened surfaces and a slightly flattened area between them. The nutrient foramen of the radius is located immediately proximal to the distal elevation. This configuration is very similar to the condition in other owls, save for the lack of the arch itself, suggesting that there might have been an unossified arch. The remaining caudal surface of the shaft is not evenly curved, but instead has the shape of a faint ridge. Measurements: maximum length (estimated), 49.

Ossa Carpi. These bones are insufficiently preserved for analysis.

Carpometacarpus. Dorsally, the os metacarpale alulare and os metacarpale majus merge into each other with almost no intervening concavity. The dorsal surface of the processus extensorius is deeply excavated (Fig. 5). The sulcus tendineus of the os metacarpale majus is comparatively broad and extends over approximately two-thirds of the length of the bone. The os metacarpale majus and os metacarpale minus are more or less parallel and of equal length distally. The spatium intermetacarpale is long and narrow. The proximal and distal synostoses seem to be rather short, but it cannot be ascertained whether or not a free processus intermetacarpalis existed. Measurements: maximum length, 24±; distal breadth, 3.

Phalanx Proximalis Digiti Majoris. The pila cranialis is divided into two blunt crests by a shallow longitudinal furrow. Both crests expand at their distal end into cranially projecting processes. The flattened caudal wing of the bone is not fenestrated. It is constricted craniocaudally just proximal to its distal end, as in *Phodilus* and genera of Strigidae. Its caudal border is curved smoothly proximally, as in *Tyto* and *Phodilus* (Ford, 1967). Measurements: maximum length, 9.5.

Phalanx Distalis Digiti Majoris. The left bone is visible cranioventrally, but it offers no special information beyond that of being strigiform. Measurements: maximum length, 9.

Phalanx Digiti Minoris. The processus for the attachment of m. flexor digiti minoris is very close to the proximal articulation, as in other owls. The bone seems to be comparatively stouter than that in *Tyto*. Measurements: maximum length, 5.

Digitus Alulae. This digit is sufficiently preserved only on the right wing. The slender proximal phalanx does not display any peculiar features, but another small conical ossicle lies on the distal fragment of the carpometacarpus on the counter-slab near to the distal end of the proximal phalanx (Fig. 5). This ossicle might be a dislocated os prominens, although one cannot preclude that it is a distal phalanx. Measurements: length of proximal phalanx, 7; length of the distal ossicle, 1.5.

Pelvis. The fragments of these bones are so crushed and deformed that no unambiguous analysis is possible.

Femur. Both femora are lost, with the exception of a small distal fragment of the right femur.

Tibiotarsus. The crista cnemialis cranialis is proximodistally rather short. Its border does not curve smoothly to join the shaft but turns sharply, forming a distinct angle, thus approaching the condition in *Tyto* and *Phodilus*. The distance between the tuberositas retinaculi mm. extensorum and the proximal border of the condylus medialis approximately equals the maximal distal breadth of the bone. The crista fibularis is comparatively short. In lateral and medial view, the shape of the condyles very closely resembles that in *Phodilus* and *Necrobyas*. The condylus medialis projects caudally with its proximal border at almost right angles to the shaft, whereas the condylus lateralis is caudally more evenly curved, fusing at a very obtuse angle with the shaft. The sulcus cartilaginis tibialis is comparatively shallow and broad. Measurements: maximum length (estimated), 53; craniocaudal depth of condylus lateralis, 5.5; craniocaudal depth of condylus medialis, 6.5.

Fibula. Only the corpus fibulae of the right leg is preserved. It is comparatively long, extending distad almost to the tuberositas retinaculi mm. extensorum. The distal end seems to be unfused, but a small longitudinal ridge with a proximal surface of fracture on the shaft of the tibiotarsus suggests that both bones were linked synostotically.

Tarsometatarsus. The tarsometatarsi are among the best-pre-

Figure 6. *Palaeoglaux artophoron* n. sp. Pes. **1–4,** sequence of toes; **5,** fossa musculi flexoris hallucis brevis. 2.96×.

served bones of the specimen (Figs. 1, 6). The overall configurations of the bone is clearly "tytonid," as exemplified by the large surface for the attachment of m. flexor hallucis brevis. Ballmann (1973:31) considers this to be one of the unmistakable features of the family Tytonidae. Unfortunately, most of the dorsal aspect is hidden from view, so nothing can be said about the presence or absence of an arcus extensorius.

Compared to a complete tarsometatarsus of *Necrobyas rossignoli* Milne-Edwards 1892, the tarsometatarsus of *Palaeoglaux artophoron* can be distinguished by the following features: Shaft somewhat shorter and distinctly more slender; crista lateralis hypotarsi posteriorly shorter and more rounded; crista medialis hypotarsi with proximal edge only a little narrower than the posterior edge and lateral face only very slightly bent laterad; transition between fossa m. flexoris hallucis brevis and sulcus flexorius very smooth and only slightly convex, thus the sulcus flexorius is proximally rather shallow, but deep distally; trochlea metatarsi II with proximal border more prominent medially and with plantar wing shorter; and fossa metatarsi I is situated more distally, i.e., closer to trochlea metatarsi II.

In contrast to the condition in *Tyto alba,* in *Palaeoglaux* and *Necrobyas* the foramen vasculare distale is situated more proximally than the dorsoproximal border of the trochlea metatarsi III. A short (5 mm) ossicle that might be the ossified part of a flexorial tendon can be seen in the sulcus flexorius of the left tarsometatarsus. Measurements: maximum length, 30.5; maximum distal breadth (estimated), 7; cranioplantar depth of the shaft laterally, 2.

Digiti Pedis. All of the toes are more or less completely preserved (Fig. 6). They differ from the toes of *Tyto* spp. by the following characters: Phalanx 1 digiti III proportionally longer; penultimate phalanges digitorum II–IV with plantar borders forming a slight convexity distal to the middle of the shaft in medial and lateral view (in *Tyto* spp. the convexity reaches proximad to about the midpoint of the shaft), and with dorsal borders of the capitula not flaring upward dorsally, but approximately forming the extension of the dorsal border of the shaft; phalanx 4 digiti IV with plantar border of capitulum semicircularly rounded in lateral view, whereas it is more or less oval in phalanx 2 digiti II and phalanx 3 digiti III; and phalanx distalis with tuberculum flexorium rather long proximodistally and in plantar view roughly dumbbell-shaped (Figs. 6, 7). Measure-

ments: maximum length: digiti I phalanx 1, 9; phalanx 2, 8; digiti II phalanx 1, 7.5; phalanx 2, 12.5; phalanx 3 (estimated), 9; digiti III phalanx 1, 5; phalanx 2, 6.5; phalanx 3, 11; phalanx 4, 9; digiti IV phalanx 1, 3±; phalanx 2, 2±; phalanx 3, 3; phalanx 4, 9.5; phalanx 5, 9.5.

Feathers. Fragments of at least eight primaries and some secondaries of the left wing are preserved as dark shadows. Shafts, barbs, and barbules can be discerned in some places, but no microstructures are recognizable. The outermost primary, lacking its tip, measures 70 mm from the tip of digitus major. Very peculiar are remnants of feathers from the trunk, most probably from the back. Numerous ribbon-like feathers are arranged there in a dense layer, partly melded into each other like a pulpy matrix (Fig. 8). These feathers are barely 1 mm wide, but at least 2 cm long, with a slender shaft. The vane appears to be membranous, without barbs, but this might be a result of diagenetic processes (see Discussion).

DISCUSSION

OTHER GENERA OF FOSSIL OWLS

Only a few genera belonging to the families Ogygoptyngidae Rich and Bohaska 1981, Sophiornithidae Mourer-Chauviré 1987, and Protostrigidae Wetmore 1933 are of the same age or older than the new Messel owl. *Ogygoptynx* Rich and Bohaska 1976 is known only from a single tarsometatarsus, which differs from that of *Palaeoglaux* in that its plantar metatarsal groove is very shallow, in that it lacks a lateral wall near the proximal end (in *Palaeoglaux* the medial wall is more flattened), and by having the crista lateralis hypotarsi directed laterally.

Palaeoglaux is easily distinguished from *Sophiornis* Mourer-Chauviré 1987 by its tarsometatarsus, which has a sulcus extensorius and is more slender.

Among the Protostrigidae, *Oligostrix rupelensis* Fischer 1983 is similar in size to *Palaeoglaux artophoron,* but these owls can be distinguished by the following features. In *Oligostrix* Fischer 1983, as in all genera of Protostrigidae, the condylus medialis tibiotarsi is very broad lateromedially and much broader than the condylus lateralis, particularly in caudal view. In *Palaeoglaux,* the condylus medialis is much narrower and in caudal view only somewhat broader than the condylus lateralis. The tuberositas retinaculi musculi fibularis on the condylus lateralis is very strong and prominent in *Oligostrix* but hardly detectable in *Palaeoglaux*. The genus *Minerva* Shufeldt 1915 is also distinguished from *Palaeoglaux* by the specialized phalanx 2 of digitus I (Mourer-Chauviré, 1983, 1987). *Eoglaucidium pallas* Fischer 1987 from Geiseltal, known only from the humerus, was classified with the Strigidae. In *Palaeoglaux artophoron,* the humerus is straighter and more slender; it has a more prominent tuberculum ventrale and margo dorsalis. Distal to the crista bicipitalis, the shaft is smoothly rounded, whereas in *Eoglaucidium* it is slightly ridged. Mlíkovský (this volume) may be right in assuming that *Eoglaucidium* is not an owl.

According to Mourer-Chauviré (1987), the family Tytonidae comprises eight genera in five subfamilies: Tytoninae (*Tyto* Billberg 1828), Phodilinae (*Phodilus* Geoffroy Saint-Hilaire 1830), Necrobyinae (*Necrobyas* Milne-Edwards 1892, *Nocturnavis* Mourer-Chauviré 1987, *Palaeobyas* Mourer-Chauviré 1987, *Palaeotyto* Mourer-Chauviré 1987), Selenornithinae (*Selenornis* Mourer-Chauviré 1987), and Palaeoglaucinae (*Palaeoglaux* Mourer-Chauviré 1987).

The new Messel owl differs from *Tyto, Phodilus, Necrobyas,* and *Palaeotyto* by the pneumatic coracoideum and many other features. *Palaeobyas* is known only from the tarsometatarsus, which is large and stout, very different from that of *Palaeoglaux*. *Nocturnavis* is known from the humerus, which has a tytonid character and is similar to that of *Necrobyas*. The humerus of the new owl differs from *Nocturnavis* in the overall configuration of its proximal end (see description) and by having the distal end only moderately expanded dorsoventrally. *Selenornis* is known from the distal end of the tibiotarsus, which has very different proportions from that of *Palaeoglaux*.

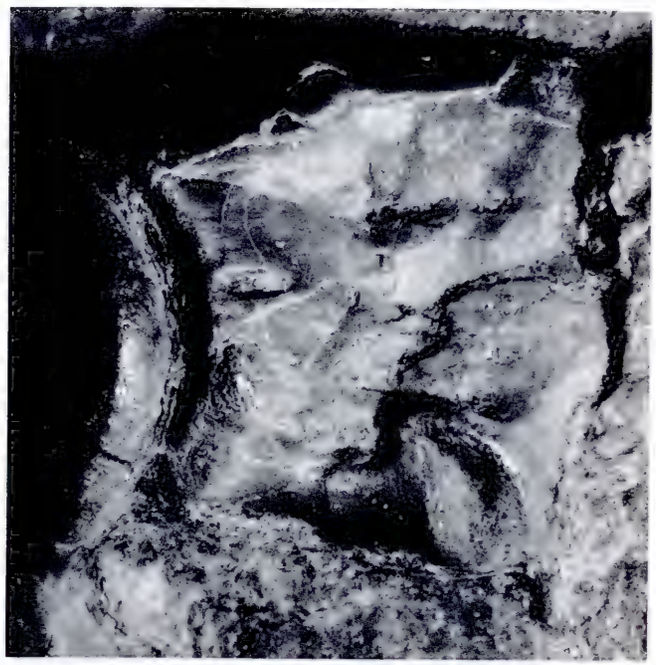

Figure 7. *Palaeoglaux artophoron* n. sp. Tuberculum flexorium phalangis distalis digiti II of the left pes. 16.65×.

Palaeoglaux is exceptional in the combination of its characters, in that it has a tarsometatarsus similar to that in *Necrobyas* but is very different in other respects. The most striking features of *Palaeoglaux* are the pneumatic coracoideum and the narrow proximal end of the ulna, the latter being described by Mourer-Chauviré (1987:114) as ". . . un peu comme celle des Galliformes . . ."

THE STATUS OF *PALAEOGLAUX*

In her excellent paper on the owls of the Phosphorites du Quercy, Mourer-Chauviré (1987) placed the genus *Palaeoglaux* in its own subfamily Palaeoglaucinae and considered this group to be the sister-group of the remaining members of the Tytonidae. The definition of this subfamily was based mainly on characters of the coracoideum, which according to Mourer-Chauviré (1987: 114) approach those of the Strigidae. The osteology of *Palaeoglaux* does indeed display a combination of tytonid and strigid characters in addition to autapomorphies. Tytonid characters are associated mainly with the tibiotarsus and tarsometatarsus, whereas strigid characters are displayed by the sternum, coracoideum, and the forelimbs (see description).

It is very tempting to regard *Palaeoglaux* as an early genus of the Strigidae. The families Tytonidae and Strigidae are usually considered to be sister-groups, this implying that they are of the same age. This assumption is still not supported by the fossil

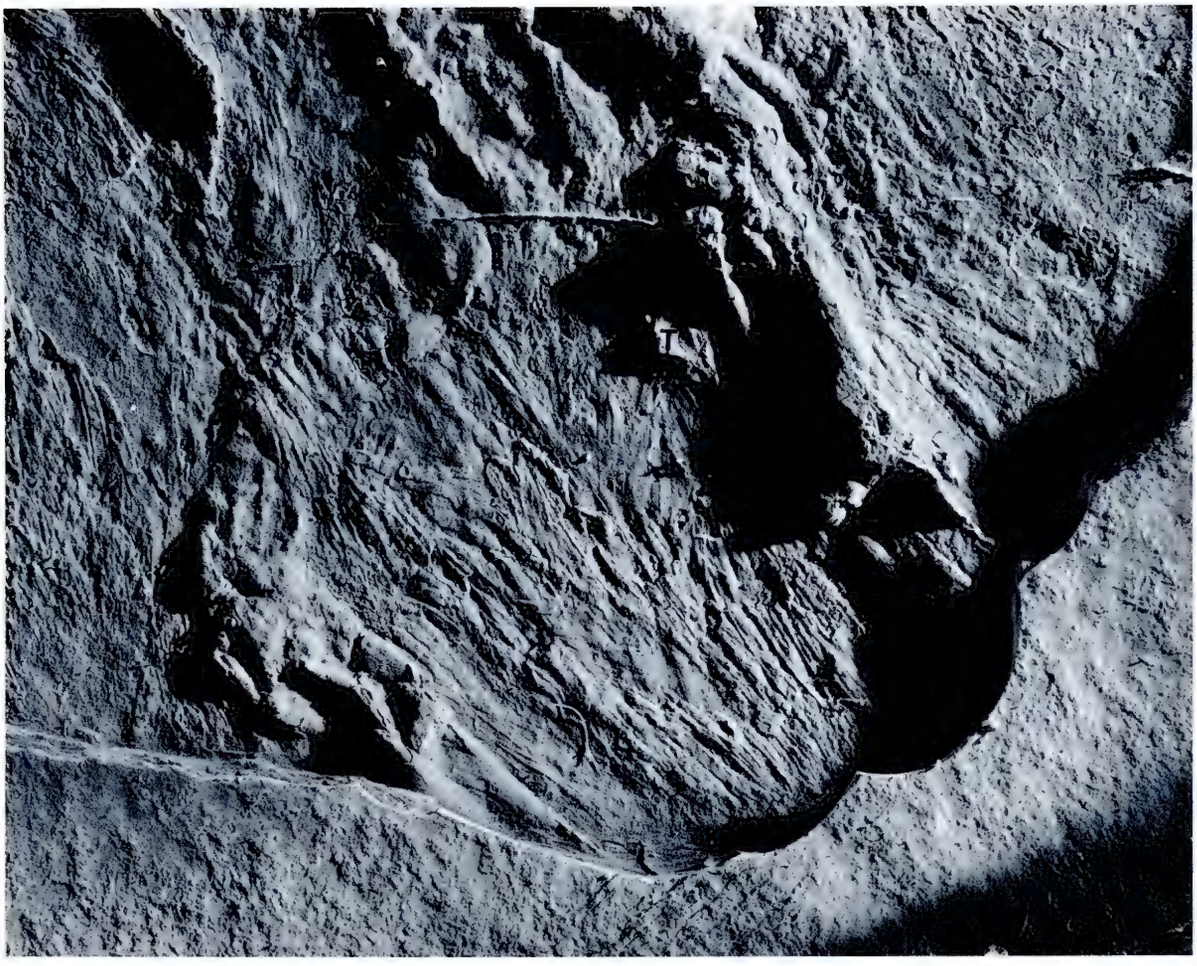

Figure 8. *Palaeoglaux artophoron* n. sp. Dense layer of narrow ribbon-like feathers. **T**, proximal end left tibiotarsus. 2.79×.

record because the earliest tytonids are known from the Eocene and the supposed earliest strigids are found as late as the Miocene (Mourer-Chauviré, 1987). It is possible, therefore, that *Palaeoglaux* represents the first evidence of Eocene strigids, as predicted by the sister-group hypothesis.

Unfortunately, the anagenetic polarity of the characters in question is unknown. This means that classifying *Palaeoglaux* with the Strigidae or the Tytonidae would anticipate the phylogenetic evaluation of the characters. Classifying *Palaeoglaux* with the Tytonidae implies that the characters shared by *Palaeoglaux* with the Strigidae are symplesiomorphies, and vice versa. Therefore, I prefer, in accordance with the predominantly typological classification of owls, to place *Palaeoglaux* in a separate family, the Palaeoglaucidae. The phylogenetic relationships of owls are clearly unsettled and present a challenge for further research.

As far as I can determine, only three osteological features can be interpreted as autapomorphies in *Palaeoglaux*. These are the peculiar shape of the proximal end of the ulna and the tuberculum flexorium of the ungual phalanges, and the relatively strong margo caudalis humeri. The conditions of these features are unknown for the families Ogygoptyngidae and Sophiornithidae because the requisite bones have not yet been found.

The peculiar feathers from the body plumage of *Palaeoglaux* may also be an autapomorphy, but because nothing is known of the plumage of other fossil owls this is pure speculation. Nonetheless, the feathers deserve attention. Remnants of soft body parts are preserved in Messel as "bacterial copies." Wuttke (1983, 1988) described the chemical aspect of these processes, where vast numbers of minute petrified bacterial bodies are left in place of histological details. Sometimes the space between the fossilized bacteria is infiltrated with organic matter to such a degree that the original structures become more or less blurred. The latter may have happened to the feathers in question, giving them a membraneous or "melded" appearance. There are only some very faint traces of a texture that suggests that the vanes consisted of barbs. Narrow, elongated contour feathers are known from species of several families, e.g., Phasianidae, Cotingidae, Paradisaeidae, and in all cases they play a role in visual display. However, ornamental plumes would have been very unusual in a nocturnal bird. Perhaps these early owls were more diurnal in habits than their modern counterparts.

Finally, although the reevaluation of characters defining families and subfamilies of owls is beyond the scope of the present work, at least two features should be discussed briefly.

The osseous arch of the radius seems to be a unique character of owls. Bock and McEvey (1969) supposed that it exists in all modern species of owls, but there are some exceptions. A. Kar-

khu (pers. comm.) did not find an osseous arch in *Glaucidium passerinum*, *G. siju*, or *Surnia ulula*. K. Campbell (pers. comm.) found "that the spp. of *Glaucidium* often did not have an osseous arch." In a spirit specimen of *G. brasilianum*, I found the arch made of soft connective tissue. Also, the consistency of the arch seems to vary in the Bay Owl, *Phodilus badius*, of which only a few skeletons exist in collections. Two of these were examined. One specimen (Museum of Vertebrate Zoology, Berkeley, MVZ 154170) displayed "slight bony crests on each radius which may have supported such an arch . . ." that "may have been broken off during specimen preparation (D.A. Bell, pers. comm.)." The second specimen (National Museum of Natural History, Washington, D.C.) has a "slight ridge or crest" that is "really evident only on the right radius and not on the left" (S.L. Olson, pers. comm.). My later examination of this specimen confirmed that the left radius did not have any trace of a bony arch. The arch seems to be lacking also in many prepared specimens of other species. However, in all such specimens that I examined, marks of excessive "cleaning" could be found. In some cases, the arches were cut away with a scalpel.

We do not know whether or not the bony arch existed in the fossil groups previously mentioned because the proximal part of the radius is not preserved in those owls.

On the basis of the evidence at hand, the arch as such seems to be a synapomorphic character of owls. Its ossification, or the secondary loss of ossification, may, however, have happened several times independently.

The os prominens is lacking in the family Tytonidae, but it occurs as an apparent apomorphy of the family Strigidae. Thus, if the small ossicle of the manus of *Palaeoglaux artophoron* was an os prominens, it would strongly support the hypothesis that *Palaeoglaux* pertains to the Strigidae. If the small ossicle is instead a distal phalanx, then it would be a plesiomorphy and it would not indicate any special phylogenetic relationship.

SUMMARY

The Eocene owl *Palaeoglaux artophoron* new species from the oil shales of Messel provides further evidence that the genus *Palaeoglaux* displays a mixture of tytonid and strigid characters. Pending further discoveries, placing the genus into its own family, the Palaeoglaucidae, appears to be the most appropriate action.

ACKNOWLEDGMENTS

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A NEW SPECIES OF *MESSELORNIS* (AVES: GRUIFORMES: MESSELORNITHIDAE) FROM THE MIDDLE EOCENE GREEN RIVER FORMATION

Angelika Hesse

ABSTRACT. A new taxon of the family Messelornithidae, *Messelornis nearctica* new species, is described from the Middle Eocene Green River Formation of Wyoming based on a slightly disarticulated complete skeleton on a slab. Taxonomic placement of the holotype to genus and family is based on the morphology of the skull and wing bones. *Messelornis nearctica* is distinguished from the type species of the family Messelornithidae, *Messelornis cristata* Hesse 1988, by differences in the proportions of the wing and leg bones. The morphology of the sternum and pelvis of the Messelornithidae indicates closest affiliation with the superfamily Eurypygoidea, suborder Rhynocheti within the Gruiformes.

ZUSAMMENFASSUNG. Ein neues Taxon der Messelornithidae, *Messelornis nearctica* n. sp. aus der mitteleozänen Green River Formation von Wyoming wird beschrieben. Der Beschreibung liegt ein vollständiges, leicht disartikuliertes Skelett auf einer Kalkplatte zugrunde. Die taxonomische Stellung des Holotypus in Gattung und Familie basiert auf der Morphologie des Schädels und der Flügelknochen. *Messelornis nearctica* unterscheidet sich von der Typusart der Messelornithidae, *Messelornis cristata* Hesse 1988 hauptsächlich durch andere Proportionen der Flügel- und Beinknochen. Die Morphologie des Sternum und des Beckens der Messelornithidae zeigt ihre Zygehörigkeit in die Überfamilie Eurypygoidea, Unterordnung Rhynocheti innerhalb der Gruiformes.

Key words: *Messelornis,* Messelornithidae, Eocene, Rhynocheti, Green River Formation.

INTRODUCTION

The fossil birds known as Messel rails are members of an extinct family, the Messelornithidae Hesse 1988, which are limited to the lower Tertiary (Eocene, Oligocene) of Europe (Germany, France) and the Eocene (Green River Formation, United States) of North America. The family Messelornithidae belongs within the superfamily Eurypygoidea of the order Gruiformes (Hesse, 1988).

Three species of *Messelornis* are recognized to date: *Messelornis cristata* Hesse 1988, the type species, from the Eocene oil shale of Messel; the new species described herein, from the Green River Formation of the United States; and an undescribed species from the Eocene–Oligocene phosphorite deposits of Quercy, France.

Osteological terminology follows Baumel (1979).

SYSTEMATICS

Order Gruiformes (Bonaparte 1954)

Characters of the order are the following (Hesse, 1989): humerus head with limited pneumatization; humerus with small fossa pneumotricipitalis, ending below or inside the tuberculum ventrale; and fourth phalanx of digit IV longer than the third phalanx.

Suborder Rhynocheti (Sharpe 1891)

The suborder is characterized by a short, broad pelvis, with a deep recessus iliacus on each side (Hesse, 1990).

Superfamily Eurypygoidea Shufeldt 1915

The superfamily is characterized by a short, broad sternum, with two to three notches on each side (Hesse, 1989).

Family Messelornithidae Hesse 1988

Family characters are as follows (Hesse, 1989).

Skull with nostrils extending very far anteriad, almost to the tip of the premaxillary; nostrils subdivided by an incomplete, long and high internasal septum; upper jaw with assumed two bending zones, one caudal to the upper jaw symphysis and the other rostral to the upper jaw base, each bending zone recognizable by a thinning of the upper jaw bar [assuming a third bending zone located on the nasalia, a double rhynchokinesis (Zusi, 1984) could have existed]; orbits small; annulus ossicularis sclerae of small diameter, composed of dorsoventrally broad ossicula sclerae; cavitas tympanica small; and foramen magnum directed ventrad.

Cervical vertebrae short.

Humerus with shaft arched in lateral and caudal direction, with proximal and distal ends much broader than the shaft; eminentia m. latissimi dorsi prominent.

Ulna compact, arched caudad, with olecranon short, broad, and blunt; tuberculum carpale developed as a high, sharp ridge; sulcus radialis deep and narrow; and proximal dorsal and caudal flank forming large angle of about 45 degrees.

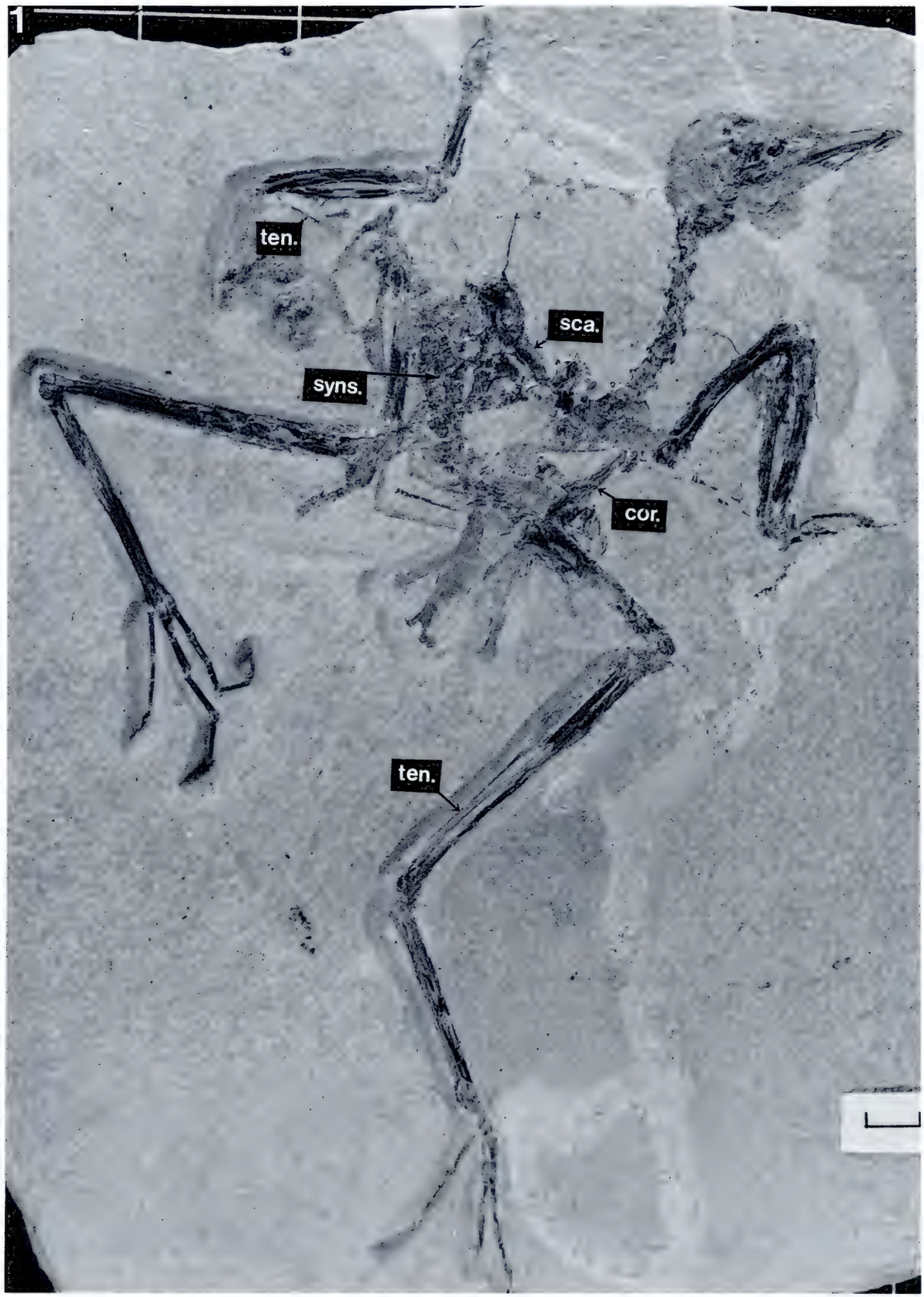


Figure 1. *Messelornis nearctica* n. sp. Holotype, SMF Av 406. **Cor,** coracoid; **sca.,** scapula; **syns.,** synsacrum; **ten.,** ossified tendon. Scale = 1 cm.

Radius compact, with distal end broadened and arched; radial tuberculum aponeurosis low; and os carpi radiale small relative to os carpi ulnare.

Carpometacarpus with trochlea carpalis short and broad, with ventral side almost spherical and dorsal side elliptical; processus extensorius long and broad; dorsal side of trochlea carpalis and processus extensorius including a large angle of about 100 degrees; processus pisiformis consisting of two rises, with a high cranial ridge and a low, pyramid-shaped caudal ridge; proximal os metacarpale minus with a high processus, just distal to the synostosis; and spatium intermetacarpale broad and long.

Tarsometatarsus with shaft straight, trochlea III short and broad; trochlea metatarsi II and IV ending distally at about the same distance.

Femur and middle toe both shorter than tarsometatarsus.

Messelornis Hesse 1988

TYPE SPECIES. *Messelornis cristata* Hesse 1988.

INCLUDED SPECIES. Type Species; *Messelornis nearctica* new species.

EMENDED DIAGNOSIS. Humerus with fossa pneumotricipitalis with small foramen pneumaticum, taking up only about one-fourth of the total size of the fossa pneumotricipitalis. The presence or absence of a furrow between the foramen vasculare distale and incisura intertrochlearis lateralis of the tarsometatarsus is interspecifically variable and, thus, not of value for generic diagnosis, in contrast to statement in original diagnosis (Hesse, 1988).

Messelornis nearctica new species

Figures 1–10

HOLOTYPE. Complete skeleton, slightly disarticulated, on a slab, more or less crushed, Forschungsinstitut Senckenberg Museum SMF Av 406. Skull and first cervicals broken away and lying isolated beneath the body skeleton. Postcranial skeleton largely in primary articulation, except for the pelvis, which is broken with the parts variously spread out; the right leg, which has come away from the pelvis; and the left forearm, which lies somewhat distant from the humerus.

DIAGNOSIS. As for genus, plus humerus a little shorter than ulna and carpometacarpus short relative to total length of wing (Fig. 1). Holotype differs from *Messelornis cristata* by having tarsometatarsus with tuberositas m. tibialis cranialis, internal tubercle, small, elliptical, short, and narrow, with flattened surface, and exterior tubercle smaller, very low, short, narrow, triangularly shaped, and not segmented; sulcus extensorius long, narrow, and deep, extending distad almost to trochlea metatarsi III (Fig. 9); furrow between foramen vasculare distale and incisura intertrochlearis lateralis; and toes longer and more slender.

TYPE LOCALITY. 15 km south of Diamondville, southwestern Wyoming.

HORIZON AND AGE. Green River Formation, Middle Eocene (Grande, 1980).

MEASUREMENTS (mm). Measurements are after Driesch (1976). The crushed condition of the specimen does not permit a complete set of measurements, and some of the measurements given are estimates.

Skull: length, 40±; bill length, 14. Fifth cervical vertebra: length, 5; width, 3.5. Thoracic vertebra: length, 5. Sternum: length, 36±; width, 12. Coracoid: length, 19. Humerus: length, 35.5; proximal width, 10; distal width, 7; shaft diameter, 3.5. Ulna: length, 36; proximal width, 4.5; distal width, 4; shaft diameter, 3. Radius: length, 33.5; proximal width, 2.5; distal width, 2.5; shaft diameter, 2. Carpometacarpus: length, 19; proximal width, 5.5; midpoint width, 3.5, distal width, 3. Digitus alulae, phalanx 1: length, 7. Digitus major, phalanx 1: length, 8.5. Digitus minor: length, 3.2.

Femur: length, 35; proximal lateral width, 7; distal lateral width, 5; shaft diameter, 4. Tibiotarsus: length, 63; proximal lateral width, 9.5; proximal medial width, 10; distal lateral width, 4.5; distal medial width, 5; shaft diameter, 4. Tarsometatarsus: length, 46; proximal dorsal width, 6.5; distal dorsal width, 5.5; shaft diameter, 3.

Tarsal digits, total length: II, 22 (9+8+5); III, 34 (10.5+9+8.5+6); IV, 27.3 (7+5.5+5+5.3+4.5).

Overall, *Messelornis nearctica* new species appears to have been similar in height to the Water Rail, *Rallus aquaticus* Linnaeus 1758.

ETYMOLOGY. *nearctica*, after Nearctic (North America), based on type locality.

DESCRIPTION. The complete skeleton of *Messelornis nearctica*, SMF Av 406, has been preserved, with the exception of the furcula, the left coracoid, the right scapula, the claws of the thumbs, and both first toes. The bones are each only partially visible because the skeleton is preserved in a slab.

In the right cavitas tympanica lies a small, stick-shaped bone that might be a relict of the columella auris.

The occipital condyle of *Messelornis nearctica* is small and spherical, only slightly broader than high, similar to that in *M. cristata*.

Cervical vertebrae 1–8 are articulated with the skull, but they are broken away from the postcranial skeleton.

→

Figure 2. *Messelornis nearctica* n. sp. Holotype, SMF Av 406. Skull. Triangles indicate bending zones of upper jaw. Arrow indicates a relict of the columella auris. Scale = 1 cm.

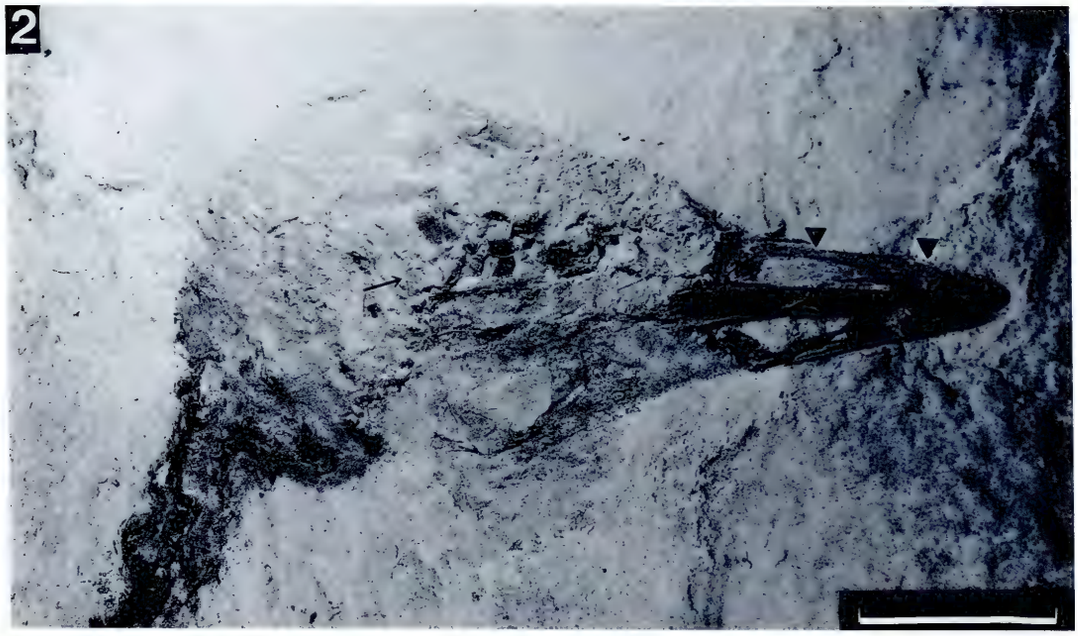
Figure 3. *Messelornis nearctica* n. sp. Holotype, SMF Av 406. Sternum. Scale = 1 cm.

Figure 4. *Messelornis nearctica* n. sp. Holotype, SMF Av 406. Humerus. **For. pneu.,** foramen pneumaticum; **em. m. lat. dors.,** eminentia m. latissimi dorsi. Scale = 1 cm.

Figure 5. *Messelornis nearctica* n. sp. Holotype, SMF Av 406. Ulna, in left dorsal view. **Ten.,** ossified tendon. Scale = 1 cm.

Figure 6. *Messelornis nearctica* n. sp. Holotype, SMF Av 406. Ulna, in right ventral view. **Ol.,** olecranon; **sulc. rad.,** sulcus radialis; **tub. apo.,** tuberculum aponeurosis; **tub. car.,** tuberculum carpale. Scale = 1 cm.

Figure 7. *Messelornis nearctica* n. sp. Holotype, SMF Av 406. Carpometacarpus, right, in ventral view. Arrow indicates high processus of proximal os metacarpale minus. Scale = 1 cm.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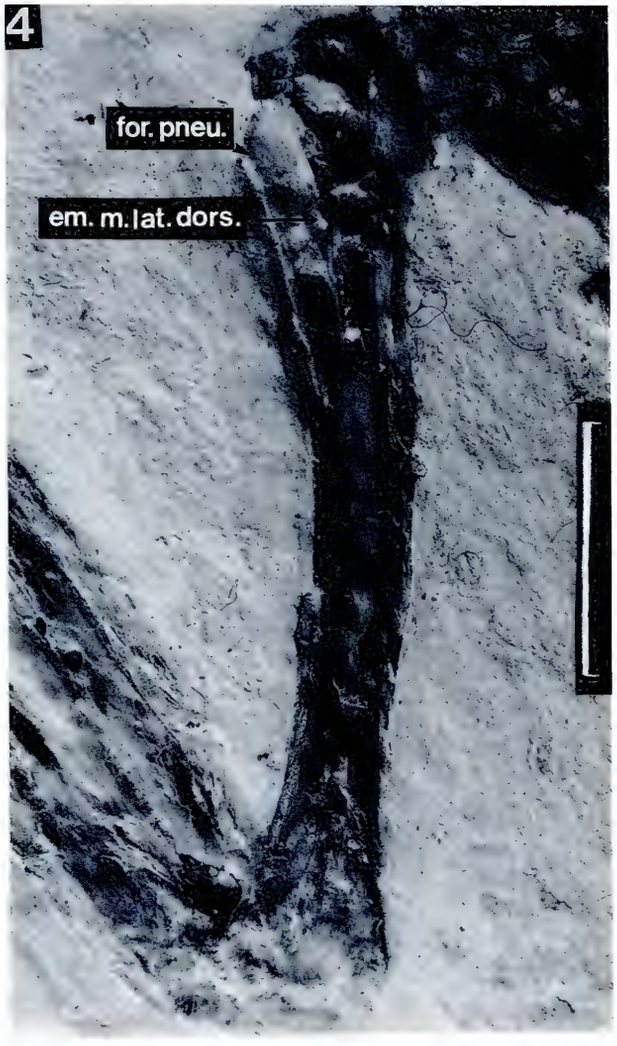
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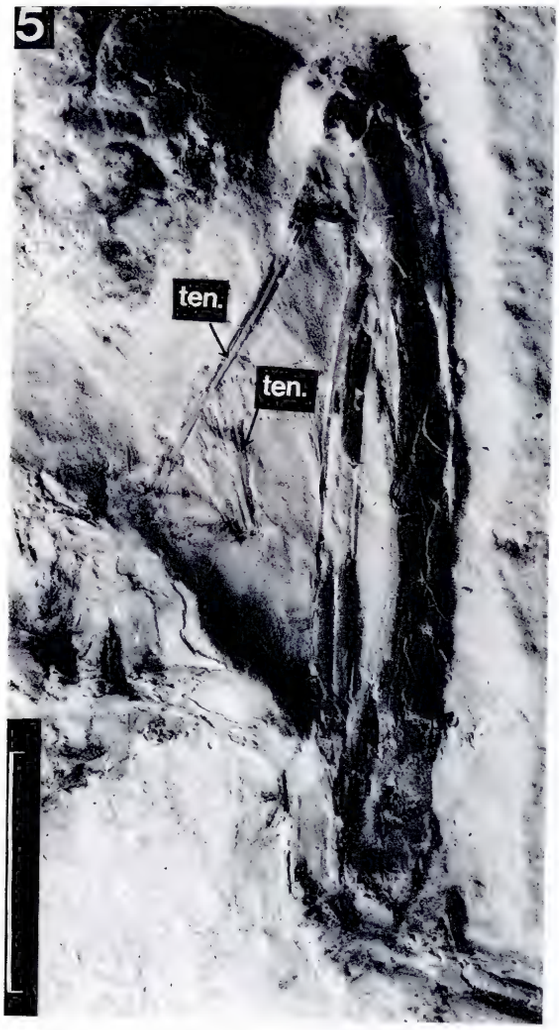
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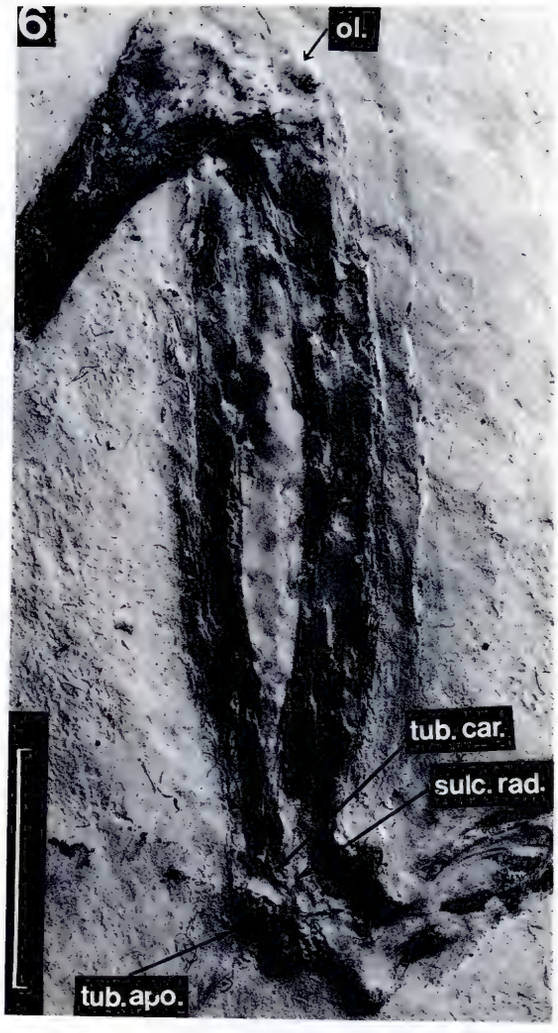
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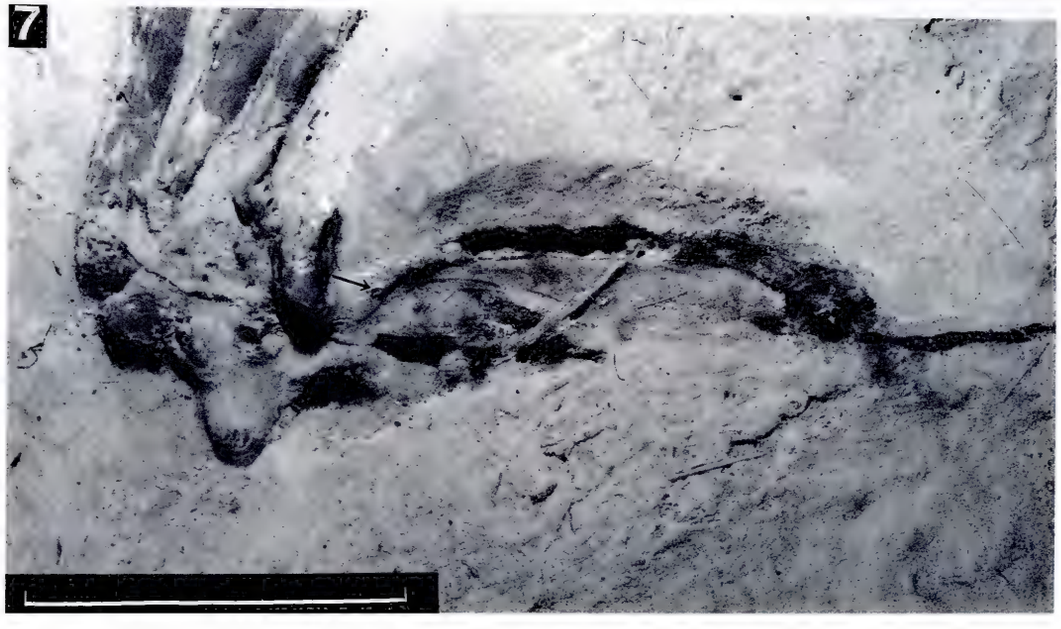
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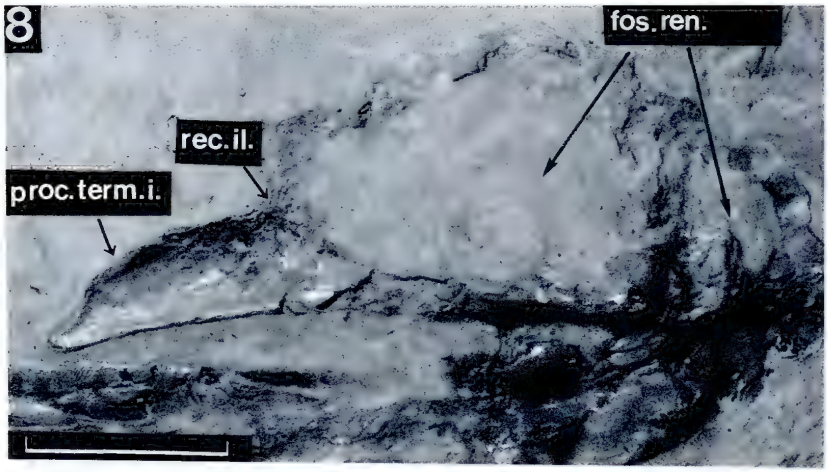

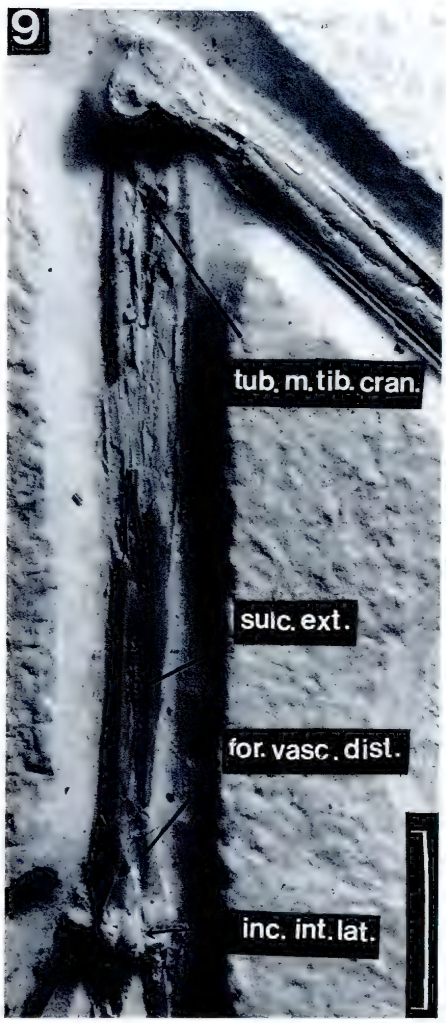

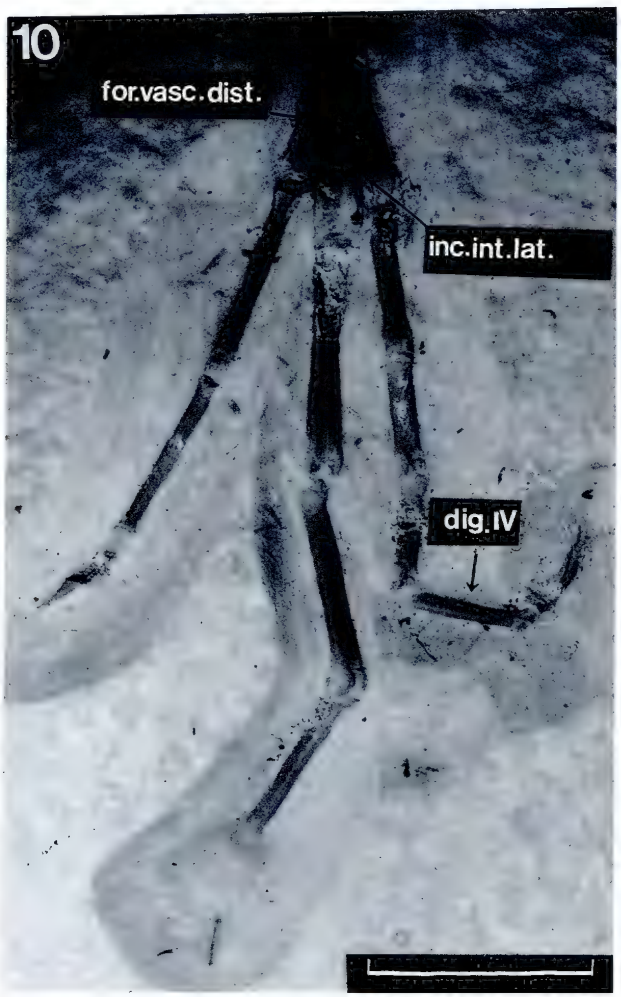

Figure 8. *Messelornis nearctica* n. sp. Holotype, SMF Av 406. Fragment of pelvis. **Fos. ren.,** fossa renalis; **proc. term. i.,** processus terminalis ischii; **rec. il.,** recessus iliacus. Scale = 1 cm.

Figure 9. *Messelornis nearctica* n. sp. Holotype, SMF Av 406. Tarsometatarsus, left, in dorsal view. **For. vasc. dist.,** foramen vasculare distale; **inc. int. lat.,** incisura intertrochlearis lateralis; **sulc. ext.,** sulcus extensorius; **tub. m. tib. cran.,** tuberositas m. tibialis cranialis. Scale = 1 cm.

Figure 10. *Messelornis nearctica* n. sp. Holotype, SMF Av 406. Foot, left, in dorsal view. **Dig. IV,** digitus IV; **for. vasc. dist.,** foramen vasculare distale; **inc. int. lat.,** incisura intertrochlearis lateralis. Scale = 1 cm.

The sternum is the best-preserved bone of the holotype. The carina sterni presses through from below (Fig. 3); its original height is not determinable. Six ribs articulate with the sternum (Fig. 3); of the posterior three, only the sternal portion can be seen. The processus uncinati have not been preserved. The total number of ribs is unknown.

The synsacrum and the thoracic vertebrae have been rotated out of their original position, through about 270 degrees. The ventral surface is exposed. The left ala ischii and left caudal ala postacetabularis ilii are missing from the synsacrum.

The pelvic pars pudenda takes in the caudal portion of the fossa renalis and about four-fifths of the total size of the fossa renalis (Fig. 8). The pars ischiadica accounts for only one-fifth of the total size of the fossa renalis. The left processus terminalis ischii is very extended, long, and broad. The left pubis is broken off, possibly lying beneath the left femur. The right pubis, the right processus terminalis ischii, and the pygostyle are missing. The alae preacetabulares ilii are broken in the middle. The rostral parts are separated and lie above the rostral sternum, at some distance from the synsacrum.

The right coracoid is crushed but can be seen to be short and moderately broad compared to the very long and narrow coracoid of *Mesitornis unicolor* (Des Murs 1845) or the short and broad coracoid of *Eurypyga helias* (Pallas 1781). The angulus lateralis is about 100 degrees. In comparison to the small, but very deep, cotyla scapularis of species of the family Rallidae, the cotyla scapularis of *Messelornis nearctica* is relatively large and shallow, similar to that in *E. helias* and *Rhynochetos jubatus* J. Verreaux and Des Murs 1860.

Only the middle portion of the left scapula is preserved. It seems to broaden caudad. The remainder of the shoulder girdle is missing.

The morphology of the humerus, ulna, radius, carpometacarpus, and carpalia is only sufficiently distinct to show the affiliation of *Messelornis nearctica* to the Messelornithidae.

The os carpi ulnare has the shape of an irregular quadrangle, with the medial and lateral branches standing just parallel to each other and separated caudally. The medial surface of the os carpi ulnare arches mediad, whereas the medial ventral surface has a furrow-shaped depression that extends caudad. Caudally, the bone is broad and flattened. The facies articularis ulnaris is relatively small and shallow, similar to that in *Rhynochetos jubatus,* in contrast to its small and deep condition in *Eurypyga helias* or its large, shallow condition in species of the family Rallidae.

The os carpi radiale has its cranial side triangle-shaped, with proximal, distal, and ventral edges, and it is deeply depressed. The ventral side is unequal and quadrangularly shaped, with a very long cranial edge and long proximal, distal, and caudal edges. In the distal half, the bone has a very shallow, broad, craniocaudally lengthened furrow, similar to that in *Rhynochetos jubatus.* Its proximal half is slightly arched ventrad.

The carpal digits are badly preserved. Only the impression of the second left carpal digit remains, and all that can be said of the third carpal digit is that it is long and slender. The base of the thumb is broad. It tapers off abruptly distally, ending in a narrow tip, which has a small, trough-shaped depression. The thumb is straight and not turned, in contrast to the condition in species of the family Rallidae.

The femur has a large diameter relative to its length (Fig. 1), with broadened proximal and distal ends.

The tibiotarsus has a long and narrow sulcus m. fibularis. The lateral side of the condylus lateralis extends over the shaft (Fig. 1), and it is flattened distally. In comparison, rallids show a well-rounded lateral side of the condylus lateralis that does not extend caudad over the shaft.

The three outer left and right tarsal digits are completely preserved in articulation with the tarsometatarsus (Figs. 1, 10).

A number of tendons of the holotype, especially of the legs and tarsals, were ossified and are well preserved, as was the case for the holotype of *Messelornis cristata* (Hesse, 1988:fig. 17, 1990). Three ossified tendons run along the plantar surface of the tarsometatarsus and the caudal surface of the distal end of the tibiotarsus. Two of the tendons split at the middle of the tibiotarsus, one into two branches and the other into at least four branches.

A number of tendons were also ossified and preserved in the left wing. Originally a tendon stretched between the ulna and the humerus, but the connection between this tendon and the humerus has been broken. Several other ossified tendons branch off this tendon and extend to the ulna and radius at right angles (Fig. 5).

DISCUSSION AND CONCLUSIONS

The construction of the foot of *Messelornis nearctica,* i.e., the phalanx 4 of digiti IV longer than the phalanx 3, shows that *M. nearctica* does not belong within the order Charadriiformes, although it bears a superficial resemblance to charadriiform birds. The latter, along with a few other groups of birds, have the phalanx 4 of digiti IV shorter than phalanx 3.

The pelvic morphology of *Messelornis nearctica* demonstrates that this taxon must be placed within the Rhynocheti, order Gruiformes. The deep recessus iliacus distinguishes the Messelornithidae, Eurypygidae, and Rhynochetidae from all other gruiform families.

The sternal morphology places *Messelornis nearctica* within the superfamily Eurypygoidea.

The following features are the main differences between *Messelornis nearctica* and *Eurypyga helias,* the only taxon of the closely related Eurypygidae, which are unknown as fossils (Olson, 1985), that reveal its place within the Messelornithidae.

The nostrils of specimens of the Eurypygidae do not extend as far rostrally and end far from the tip of the premaxillary.

The incomplete internasal septum of *Messelornis nearctica* is very extended, long, and broad (a synapomorphic feature for the Messelornithidae). In contrast, the internasal septum in specimens of the Eurypygidae is largely reduced, rostrocaudally elongated, and dorsoventrally very low (a synapomorphic feature of the Eurypygidae).

The foramen magnum of *Messelornis nearctica* is directed ventrad, whereas in *Eurypyga helias* it is directed caudad so that the cervical vertebrae and the skull in *E. helias* form a straight line.

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A NEW GALLINACEOUS BIRD FROM THE OLIGOCENE OF NEBRASKA, WITH COMMENTS ON THE PHYLOGENETIC POSITION OF THE GALLINULOIDIDAE

Timothy M. Crowe and
Lester L. Short

ABSTRACT. A new genus and species of gallinaceous bird, *Archaealectrornis sibleyi,* is described based on a humerus from mid-upper Oligocene deposits of Nebraska. Comparison with various extant and fossil species of the orders Galliformes and Anseriformes indicates that this humerus represents a primitive grouse- or pheasant-like galliform possibly related to *Gallinuloides wyomingensis* Eastman 1900, the earliest known member of the order Galliformes, and/or to contemporary Eocene–Oligocene galliforms from the Phosphorites du Quercy in southern France. It is hypothesized that *Archaealectrornis* and the other pre-Miocene galliform fossils studied are representatives of an extinct family of gallinaceous birds, the Gallinuloididae, which is the sister-group of the Phasianidae, and that similarities between members of this family and members of the Anseriformes are a result of character reversals to primitive states.

Key words: Aves, Gallinuloididae, galliform, Oligocene, Nebraska.

INTRODUCTION

Among a group of avian fossils from the Oligocene of Nebraska studied by one of us (L.L.S.) is a humerus closely resembling that of gallinaceous birds. Our aims in this paper are to determine the taxonomic status of this fossil and to comment on its possible phylogenetic affinities.

METHODS AND MATERIALS

The fossil humerus was compared qualitatively with fossil humeri and/or their descriptions listed in Brodkorb (1964:297–326) and with representatives of a broad range of material from extant galliform genera available in the American Museum of Natural History (AMNH); the Museum of Comparative Zoology (MCZ); the United States National Museum; the Natural History Museum, London; the Transvaal Museum; the South African Museum; and the Natural History Museum of Los Angeles County. We were also able to compare the fossil with described and undescribed Plio-Pleistocene material from Olduvai Gorge, Tanzania; humeri from the famous Eocene–Oligocene deposits of the Phosphorites du Quercy, southeastern France (Mourer-Chauviré, this volume); humeri from Miocene deposits at Arrisdrift, near the mouth of the Orange River in Namibia (Crowe, in press); and dozens of complete humeri from lower Pliocene deposits at Langebaanweg, just north of Cape Town, South Africa (Crowe, in press). Various anseriform humeri and descriptions and illustrations of certain fossil species of the Anseriformes were also used for comparison.

Ten measurements (Fig. 1; Table 1) were taken on the fossil humerus and humeri from one similarly sized anatid and galliforms representing all extant suprageneric taxa attributed to the Galliformes. An additional character, the development of the second pneumatic fossa, was scored for each fossil and bone (from 0 to 5, with increments of 0.5).

The approach used to analyze the mensural data is given in detail in Crowe and Crowe (1985). Mensural data were $\log_{10}$-transformed, standardized, and analyzed using the BMDP cluster analysis (P2M) program (Dixon, 1981) to determine the morphometric nearest neighbor of each humerus measured. By morphometric nearest neighbor, we mean the specimen with the lowest Euclidian distance from the humerus in question. Assuming that Euclidian distance reflects genetic similarity, we would expect that morphometric nearest neighbors are likely to be phylogenetically related, and that the fossil is most closely related to its morphometric nearest neighbor.

SYSTEMATICS

Class Aves Linnaeus 1758

Order Galliformes Temminck 1820

Family Gallinuloididae Lucas 1900

Archaealectrornis new genus

TYPE SPECIES. *Archaealectrornis sibleyi* new species.

DIAGNOSIS. A pheasant-sized galliform. A robust humerus with a very well-developed pneumatic foramen and a moderately developed second pneumatic fossa. The bicipital crest is squared-off like that of *Numida meleagris* (Linnaeus 1758) rather than rounded as in most phasianids. The capital groove is well developed, connecting directly with the second pneumatic fossa, and not separated from that depression by a ridge connecting the articular surface of the head with the internal tuberosity. The ligamental furrow is very deep, with its sides, especially the anconal side, flattened in anatid fashion. The head is thus relatively shallow and strongly undercut distally. The shaft is curved, thin at midpoint, and flaring somewhat distally. The attachment of m. pronator brevis is very strongly marked and greatly pro-

Table 1. Humerus mensural data and an estimate of the development of the second pneumatic fossa for *Archaealectrornis sibleyi*, selected fossil galliforms, a similarly sized anatid, and a range of extant galliforms. Abbreviations: M, male; F, female; L, left; R, right; see Fig. 1 legend for others.

Taxon	TL	PW	.3SW	.5SW	.6SW	DW	.5DP	DPF	ICP	ICD	DSPF
Archaealectrornis sibleyi n. sp.	77.3	20.0	10.0	7.4	8.2	16.8	5.9	7.7	2.3	5.3	2.0
Fossils											
Undescribed *Gallinuloides* sp. MCZ 2506	—	18.3	—	—	—	—	—	6.9	—	—	2.0
Undescribed phasianid Olduvai	57.0	14.3	6.7	5.2	5.2	11.3	4.3	6.0	1.5	4.6	2.0
Undescribed phasianid Arrisdrift	68.5	16.8	8.9	6.0	5.6	12.0	4.6	6.0	2.0	3.7	2.0
Paraortyx lorteti	40.9	10.1	4.4	3.4	3.4	7.8	3.0	3.0	1.3	2.5	4.0
Palaeortyx gallica	43.3	11.1	5.4	3.8	3.5	8.6	3.1	5.0	1.1	3.0	3.5
Palaeortyx brevipes	34.2	8.5	3.8	2.9	3.4	6.5	2.5	3.4	1.1	2.3	3.5
Pirortyx major	56.4	14.4	5.6	4.7	4.6	9.7	4.2	6.8	1.0	3.9	2.0
Undescribed megapode Quercy	87.7	18.5	9.2	7.6	7.3	14.7	6.8	8.6	1.4	5.4	5.0
Quercymegapodius brodkorbi	32.5	8.3	3.4	2.4	2.3	5.6	2.2	2.5	0.8	2.0	5.0
Quercymegapodius depereti	39.9	9.7	5.3	3.4	3.1	7.6	3.0	3.6	0.9	2.5	5.0
Q. depereti	36.7	10.0	4.6	3.4	3.3	7.6	3.0	3.2	1.2	2.4	5.0
Francolinus spp. Langebaanweg	53.7	13.7	6.6	4.8	4.4	9.6	4.0	5.4	1.3	3.5	2.0
Francolinus spp. Langebaanweg	58.5	14.8	7.2	5.4	4.9	10.8	4.3	7.1	1.5	4.2	2.0
Extant taxa											
Anatidae											
Anas clypeata	75.2	16.3	6.4	5.5	5.3	11.8	4.8	6.4	1.0	4.3	0.0
Megapodiidae											
Megapodius freycinet	69.1	16.6	8.5	6.3	6.2	13.9	5.2	6.0	1.3	4.8	0.0
Cracidae											
Penelope purpurascens	104.0	26.2	12.9	11.2	11.3	23.2	9.2	6.1	1.8	7.7	0.0
Crax globulosa	95.4	24.1	12.2	9.4	8.8	20.5	7.6	6.0	1.4	8.3	0.0
Ortalis vetula F-L	55.0	12.4	6.7	5.0	5.7	10.6	4.1	3.7	1.3	3.6	0.5
O. vetula F-R	55.6	12.3	6.6	4.9	5.3	10.6	4.1	3.7	1.3	3.6	0.5
O. vetula M-L	59.0	13.0	6.7	5.3	5.8	11.0	4.5	5.9	1.4	4.0	0.5
Phasianidae											
Guttera plumifera	74.1	18.8	10.1	7.7	7.3	15.2	5.6	5.3	1.4	5.3	0.0
Agelastes niger	61.3	16.6	8.7	6.8	6.4	14.3	5.6	6.1	1.3	4.8	1.0
Meleagris ocellata	97.2	25.6	11.9	9.6	8.9	20.8	7.6	7.9	2.0	7.4	0.0
Centrocercus urophasianus	88.9	23.6	9.8	8.3	7.8	16.7	6.1	9.7	2.2	6.3	1.0
Gallus varius	66.4	18.8	8.8	6.9	6.9	16.1	5.9	6.6	1.6	5.4	1.0
Phasianus colchicus	74.6	20.2	8.8	6.8	6.4	15.3	5.3	7.4	1.6	5.7	1.0
Pavo cristatus	131.3	31.1	16.6	13.3	13.3	28.2	10.9	11.9	2.4	9.6	1.0
Lophortyx californica	32.4	9.2	4.4	3.2	3.2	7.2	2.3	3.8	0.8	2.4	3.0
Tetraogallus himalayensis M-L	94.5	24.4	10.8	8.5	8.2	19.9	7.4	12.0	2.0	7.2	1.0
T. himalayensis M-R	94.3	24.5	11.3	8.6	8.3	19.9	7.5	12.5	2.2	7.3	1.5
Francolinus africanus M-L	53.9	14.0	7.1	5.0	4.6	10.9	3.9	5.3	1.6	4.0	2.0
F. africanus F-L	51.1	13.8	6.6	4.8	4.6	10.6	3.8	6.0	1.4	3.8	2.0
F. africanus M-L	52.5	13.6	6.5	4.9	4.6	10.3	4.0	5.5	1.2	3.9	2.0
F. africanus F-L	49.0	13.1	6.8	4.5	4.2	9.9	3.7	5.6	1.2	3.5	2.0
Francolinus levaillantoides M-R	54.2	14.0	6.6	5.0	4.6	11.0	4.1	6.2	1.5	3.9	2.0
F. levaillantii F-L	56.2	14.6	7.5	5.2	5.2	11.0	4.0	6.2	1.4	3.9	2.0
F. levaillantii F-L	53.1	14.2	6.6	4.6	4.6	10.8	3.5	6.0	1.4	4.0	2.0
Francolinus lathami F-L	41.6	11.5	6.2	4.0	4.5	9.0	3.5	4.4	1.0	4.0	1.5
Francolinus coqui M-L	47.0	11.5	5.0	3.8	3.7	8.4	3.3	4.8	1.3	3.4	2.0
Francolinus francolinus M-L	54.8	12.3	5.9	4.5	4.5	10.0	3.6	5.7	1.2	3.6	1.5
F. francolinus M-R	54.8	12.2	6.1	4.6	4.5	10.1	3.6	6.0	1.4	3.6	1.5
Francolinus pictus F-L	44.9	11.6	6.3	4.1	4.1	9.2	3.3	5.0	1.3	3.4	1.0
F. pictus F-R	50.0	11.5	6.5	4.1	4.1	9.2	3.3	4.7	1.4	3.2	1.5
Francolinus pondicerianus F-L	43.8	11.4	5.0	4.0	4.3	9.0	3.5	4.2	1.2	3.3	1.5
Francolinus sephaena F-L	47.3	11.7	6.2	4.4	4.6	9.6	3.7	4.6	1.2	3.5	2.0
F. sephaena F-R	47.5	11.7	6.3	4.3	4.4	9.4	3.7	4.6	1.4	3.4	2.0
Francolinus capensis M-R	69.2	18.3	9.3	6.6	6.9	13.7	5.7	8.1	1.7	5.3	2.0

Table 1. Continued.

Taxon	TL	PW	.3SW	.5SW	.6SW	DW	.5DP	DPF	ICP	ICD	DSPF
F. capensis M-L	69.3	18.0	10.4	6.6	6.6	13.9	5.8	7.8	1.6	5.3	2.0
Francolinus swainsonii F-L	57.0	14.6	7.0	5.1	5.1	11.1	4.1	6.2	1.4	4.4	2.0
Francolinus afer F-L	49.9	12.6	6.8	4.5	4.6	10.2	3.8	4.8	1.2	3.7	2.0
F. afer F-R	49.7	12.3	6.2	4.5	4.8	10.3	3.7	4.5	1.4	3.4	2.0
Francolinus squamatus L	48.0	12.2	6.5	4.5	5.1	10.1	3.7	4.2	1.7	3.6	1.5
Francolinus icterorhynchus F-L	53.2	13.4	6.7	4.8	4.7	11.3	3.9	4.7	1.3	4.2	1.5
Francolinus clappertoni M-L	57.1	14.4	7.4	5.0	6.0	11.5	4.2	5.9	1.5	4.4	2.0
F. clappertoni M-R	56.9	15.8	7.8	5.0	6.0	11.5	4.3	5.4	1.5	4.3	2.0
Francolinus bicalcaratus M-L	58.3	15.2	7.9	5.0	6.1	11.9	4.2	6.0	1.6	4.1	2.0
Alectoris graeca M-L	52.3	14.7	6.5	4.7	4.8	11.3	4.0	7.0	1.5	4.2	3.0
A. graeca M-R	52.2	14.6	6.6	4.8	4.6	11.1	3.9	6.8	1.5	4.1	3.0
Ammoperdix griseogularis L	37.3	10.8	6.0	4.4	4.1	8.4	3.3	4.5	1.0	3.2	3.0
A. griseogularis R	37.1	10.9	6.0	4.3	4.3	8.3	3.2	4.4	1.0	3.5	3.0
Ammorperdix heyi L	38.5	10.7	5.1	2.6	3.8	8.2	3.0	3.8	1.1	3.2	3.0
Rhizothera longirostris M-L	60.4	16.0	9.4	6.4	7.3	13.2	5.0	5.3	2.1	4.9	2.0
Margaroperdix madagarensis 1	45.3	10.6	5.9	3.8	4.1	8.2	2.9	5.5	1.3	3.0	3.0
Arborophila charltoni M-L	47.4	13.2	7.3	4.8	5.4	11.1	3.8	5.9	1.7	4.0	2.5
A. charltoni M-R	47.5	13.3	7.9	4.8	5.6	11.0	3.8	6.0	1.7	3.9	2.5
Rollulus roulroul L	41.8	11.9	7.3	4.2	5.0	8.9	3.3	4.4	1.3	3.7	2.0
R. roulroul R	41.8	12.0	7.1	4.2	4.8	9.1	3.2	4.2	1.5	3.5	2.0

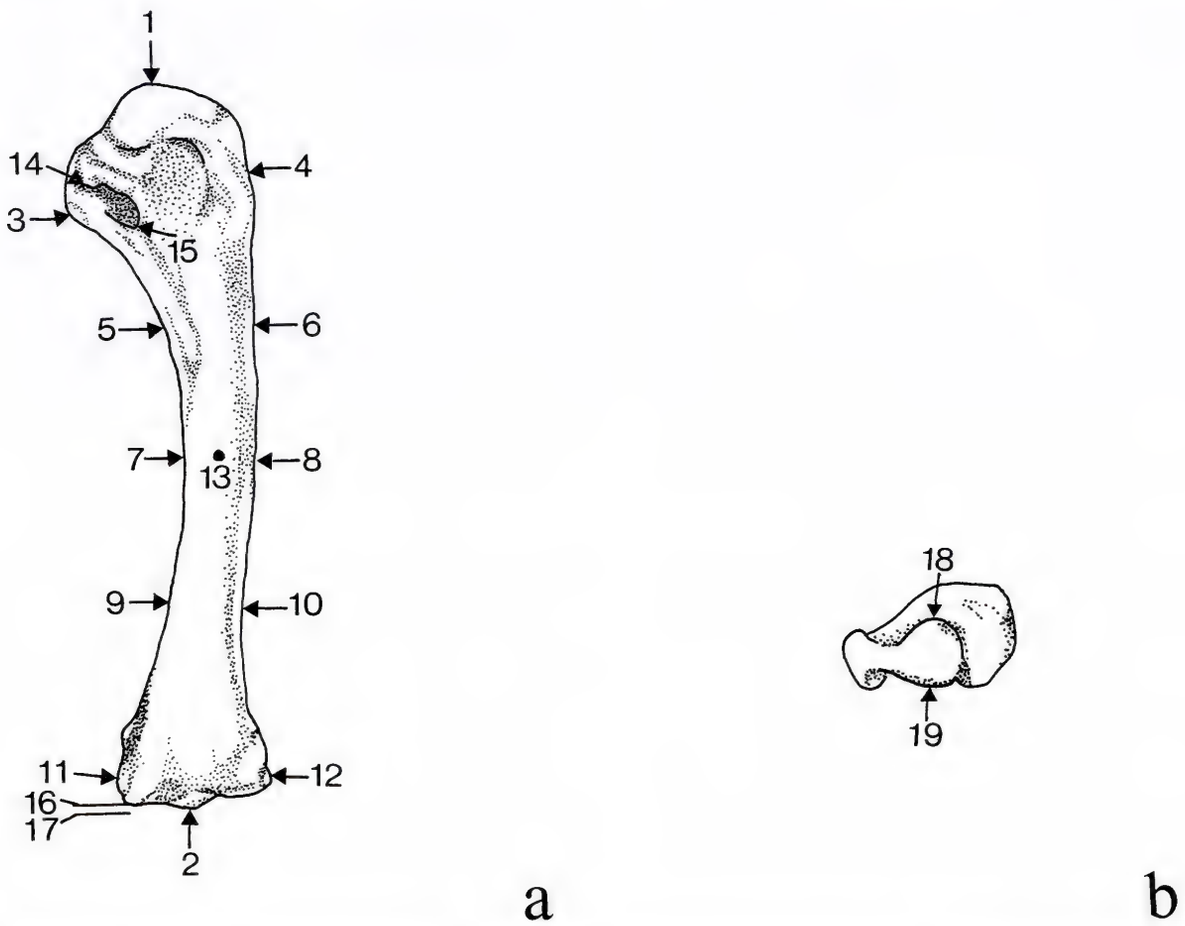

Figure 1. Measurements taken on the *Archaealectrornis sibleyi* n. gen., n. sp., humerus and humeri from extant galliforms: (**a**) anconal view, (**b**) distal view. Numbers in parentheses refer to measurement reference points. **TL,** total length (**1–2**); **PW,** proximal width (**3–4**); **.3SW,** shaft width ⅓ way down TL (**5–6**); **.5SW,** shaft width ½ way down TL (**7–8**); **.6SW,** shaft width ⅔ way down TL (**9–10**); **DW,** distal width (**11–12**); **.5DP,** shaft depth ½ way down TL (**13** to corresponding point on palmar side); **DPF,** diameter of pneumatic foramen (**14–15**); **ICP,** internal condyle projection (**16–17**); **ICD,** internal condyle depth (**18–19**); DSPF, development of second pneumatic fossa.

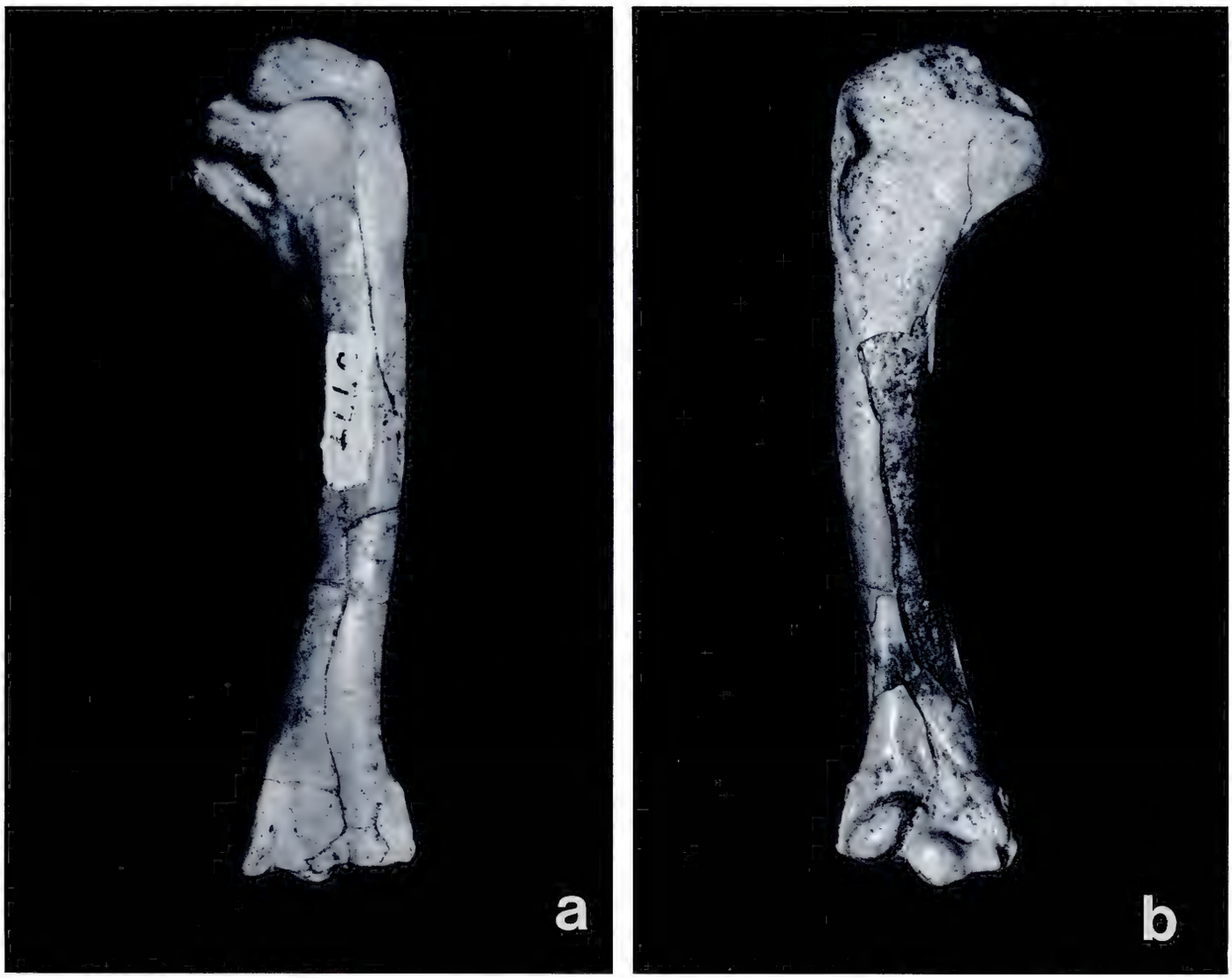

Figure 2. Anconal (**a**) and palmar (**b**) views of holotype humerus of *Archaealectrornis sibleyi* n. gen., n. sp., University of Nebraska State Museum No. 5774. Total length of holotype is 77.3 mm.

truding internally, in anconal view. The internal condyle protrudes distad, well beyond the entepicondyle and ectepicondyle.

ETYMOLOGY. *Archaealectrornis,* from Greek, meaning, approximately, ancient fowl-like bird; masculine.

Archaealectrornis sibleyi new species

Figure 2

HOLOTYPE. University of Nebraska State Museum No. 5774, a nearly complete right humerus, lacking distal portion of deltoid crest, and a 5-×-35-mm piece of the central internal palmar surface of the shaft. A cast of the holotype (AMNH 27001) is in the Department of Vertebrate Paleontology at the American Museum of Natural History.

DIAGNOSIS. As for genus.

TYPE LOCALITY. The holotype was collected on 13 July 1933 by a University of Nebraska field party headed by C.B. Schultz at 1.6 km south and 3.2 km west of Scottsbluff, Scotts Bluff County, Nebraska, northeast of U.S. Highway 86 in Sec. 34, T.22N, R.55W, 41°49′N, 103°43′W. University of Nebraska locality Sf-101.

HORIZON AND AGE. Brule Formation of the White River Group, Orella and Whitney Members. Middle to Upper Oligocene.

ETYMOLOGY. Patronymic, in honor of Professor Charles G. Sibley.

DESCRIPTION. The holotype is fractured along the shaft, but all features of both ends are clearly visible. This part of the description centers on comparison of the holotype with comparably sized humeri of four reference taxa: the cracid *Penelope superciliaris* Temminck 1815, the numidine phasianid *Numida meleagris* (Linnaeus 1758), the tetraonine phasianid *Tympanuchus cupido* (Linnaeus 1758), and an undescribed, well-preserved, proximal humerus of a putative species of *Gallinuloides* Eastman 1900 from the Oligocene (Museum of Comparative Zoology; MCZ 2506); collection site, White River, South Dakota (for measurements, see Table 1).

The holotype is about the size of a humerus of a large Prairie

Table 2. Nearest morphometric neighbors of *Archaealectrornis sibleyi,* selected galliform fossils, and *Anas clypeata.* Based on data set given in Table 1. See Methods and Materials for details on data transformation and analysis. Abbreviations: F, female; M, male.

Taxon	Three nearest extant neighbors (Euclidian distance)	Nearest fossil neighbor (distance)	Distance to *Anas clypeata*
Archaealectrornis sibleyi n. sp.	*Centrocercus urophasianus* (1.63), *Francolinus capensis* M (1.87, 2.11), *Rhizothera longirostris* (2.12)	Arrisdrift phasianid (2.70)	5.35
Undescribed phasianid Olduvai, Tanzania	*Francolinus swainsonii* F (0.43), *F. clappertoni* (0.62), *F. levaillantii* M (0.73)	*Francolinus* sp. Langebaanweg (0.75)	3.23
Undescribed phasianid Arrisdrift, Namibia	*Rhizothera longirostris* (1.51), *F. bicalcaratus* M (1.52), *F. clappertoni* M (1.81)	*Francolinus* sp. Langebaanweg (1.95)	4.14
Paraortyx lorteti Quercy	*Ammoperdix heyi* (1.65), *Francolinus coqui* M (2.26), *Lophortyx californica* (2.33)	*Quercymegapodius depereti* (0.71)	6.28
Palaeortyx gallica Quercy	*Margaroperdix madagarensis* (1.02), *Ammoperdix griseogularis* (1.09, 1.24), *F. coqui* M (1.30)	*Quercymegapodius depereti* (1.73)	5.04
Palaeortyx brevipes Quercy	*Lophortyx californica* (1.44), *Ammoperdix heyi* (1.95), *A. griseogularis* (2.81)	*Quercymegapodius depereti* (1.43)	6.91
Pirortyx major Quercy	*Francolinus africanus* M (0.96), *F. francolinus* M (1.09), *F. africanus* F (1.10), *F. levaillantii* F (1.18)	*Francolinus* sp. Langebaanweg (1.10)	3.06
Undescribed "megapode" Quercy	*F. capensis* M (2.11, 2.15), *Phasianus colchicus* (2.90), *Gallus varius* (2.98)	*Archaealectrornis sibleyi* (3.02)	5.13
Quercymegapodius brodkorbi Quercy	*L. californica* (2.32), *A. heyi* (3.53), *A. griseogularis* (4.39)	*Palaeortyx brevipes* (2.14)	8.45
Quercymegapodius depereti Quercy	*L. californica* (1.61), *A. heyi* (1.76), *A. griseogularis* (1.95)	*Paraortyx lorteti* (1.71)	6.35
Q. depereti Quercy	*A. heyi* (1.71), *L. californica* (2.05), *A. griseogularis* (2.27)	*Paraortyx lorteti* (0.71)	6.60
Francolinus sp. Langebaanweg	*F. africanus* M (0.56), *F. africanus* F (0.62, 0.68), *F. afer* F (0.75), *F. levaillantii* F (0.87)	*Pirortyx major* (1.10)	3.34
Francolinus sp. Langebaanweg	*F. swainsonii* F (0.64), *F. levaillantii* F (0.70), *F. levaillantii* M (0.76), *F. clappertoni* M (0.98)	Olduvai phasianid (0.75)	3.23
Anas clypeata	*Megapodius freycinet* (1.76), *Ortalis vetula* (2.09), *Agelastes niger* (2.62)	*Pirortyx major* (3.06)	0.00

Chicken (*Tympanuchus cupido*) or Ring-necked Pheasant (*Phasianus colchicus* Linnaeus 1758), and it is similar in shape and general appearance to the humeri of these species. The head of the fossil humerus is most similar to that of the undescribed species of *Gallinuloides* because it lacks a ridge connecting the humeral head to the internal tuberosity. This ridge is strongly marked in *T. cupido* and *P. colchicus,* but it is only extremely rudimentary in the undescribed species of *Gallinuloides.* The bicipital crest is squared off, resembling that of *Numida meleagris.* The shaft differs from those of the reference taxa in being more robust, most like the humerus of *N. meleagris.*

The distal end of the holotype is more robust, wider, and less deep than those of the three extant reference taxa. The distal end of the shaft between the tricipital grooves and the proximal end just below the internal tuberosity are also especially flattened. The curvature of the shaft resembles that observed in *Tympanuchus cupido* and *Phasianus colchicus.* The internal condyle protrudes strongly distad, i.e., as in *T. cupido* and most other tetraonines.

MORPHOMETRIC DESCRIPTION. Mensural data for the fossil and humeri from a similarly sized anatid, *Anas clypeata* Linnaeus 1758, and an array of fossil and extant galliforms are given in Table 1. The three morphometric nearest neighbors of all fossils studied (except for the undescribed *Gallinuloides* sp., which had missing data for all but three of the measurements) and of *A. clypeata* are given in Table 2. The 10 morphometric nearest neighbors in increasing order of Euclidian distance from the fossil are as follows: *Centrocercus urophasianus* (Bonaparte 1827), 1.63; male *Francolinus capensis* (Gmelin 1789) (left), 1.87; *F. capensis* (right), 2.11; *Rhizothera longirostris* (Temminck 1815), 2.12; *Gallus varius* (Shaw 1798), 2.27; *Phasianus colchicus,* 2.29; male *Tetraogallus himalayensis* G.R. Gray 1842 (right), 2.59; *T. himalayensis* (left), 2.65; and an undescribed "megapode" (3.02) from the Phosphorites du Quercy in southeastern France. Thus, with the exception of the undescribed "megapode" humerus from the Quercy deposits, which is morphometrically much closer to the humeri of *F. capensis, P. colchicus,* and *Gallus varius* (Table 2) than it is to the humerus from *Megapodius freycinet* Gaimard 1823 (4.57), the nearest morphometric neighbors of the holotype are phasianids.

In a second nearest neighbor analysis based on the three measurements for which we have data for the undescribed *Gallinuloides* sp., the 10 nearest neighbors of the holotype are as follows: *Francolinus capensis* male (right), 0.37; *F. capensis* male (left), 0.38; the undescribed *Gallinuloides* sp., 0.49; *Phasianus colchicus,* 0.95; the undescribed Arrisdrift phasianid, 1.05; *Gallus varius,* 1.10; fossil *Francolinus* sp. from Langebaanweg, 1.12; *Pirortyx major* (Gaillard 1908), 1.25; *F. bicalcaratus* (Lin-

naeus 1766) male, 1.29; and an *Alectoris graeca* (Meisner 1804) male, 1.33. This analysis reaffirms the phasianid affinities of the holotype and its strong similarity to *Gallinuloides*.

PHYLOGENETIC AND TAXONOMIC CONCLUSIONS

Phylogenetic and taxonomic diagnoses based on limited postcranial Paleogene bird fossil material are generally very problematic (Olson, 1985). Owing to the remarkable uniformity in shape, and often strong sexual size dimorphism, of the skeletons of phasianids, such conclusions are particularly difficult for "higher" galliforms (i.e., the Phasianidae, *sensu* Morony et al., 1975). For example, only a few of the more than 100 skeletal characters employed by Steadman (1980) unequivocally distinguish turkeys (Meleagridinae) from other phasianids. Nevertheless, there are a few features of the humerus that Holman (1964) and we have found useful in diagnosing galliform humeri.

First, in all extant galliforms, the capital groove is separated from the second pneumatic fossa by a projection of the articular surface of the head toward the internal tuberosity. This projection is less well developed in cracids, and it is absent in the Anseriformes, the likely sister-group of the Galliformes (Cracraft, 1981). Second, the pneumatic foramen is much larger in phasianids than in megapodes or cracids. Third, the second pneumatic fossa is moderately to well developed in phasianids but absent in anseriforms and poorly developed or absent in megapodes and cracids.

On the strength of its high overall morphometric similarity with phasianids and the undescribed *Gallinuloides* sp. and the following derived features—large pneumatic foramen, moderately developed second pneumatic fossa, and protruding internal condyle, which is characteristic of most grouse genera—the most parsimonious decision is to place *Archaealectrornis sibleyi* with *Gallinuloides wyomingensis* in the family Gallinuloididae Lucas 1900. We consider the Gallinuloididae to be the sister-group of the Phasianidae. Although the proximal end of the humerus of the type specimen of *G. wyomingensis* is badly crushed, the well-preserved proximal humerus of the putative species of *Gallinuloides* from the collections of the Museum of Comparative Zoology referred to earlier has a large pneumatic fossa, a moderately developed pneumatic foramen, and a virtually uninterrupted capital groove. Thus, the uninterrupted capital groove that gives the head of the holotype a somewhat anseriform shape is considered to be a reversal to a primitive condition and becomes a synapomorphy for the family.

Since the fossil humeri studied representing *Paraortyx lorteti* Gaillard 1908, *Pirortyx major, Quercymegapodius depereti* (Gaillard 1908), and *Q. brodkorbi* Mourer-Chauviré this volume, from the Eocene–Oligocene deposits of the Phosphorites du Quercy in southeastern France also have an uninterrupted capital groove, phasianid nearest morphometric neighbors (Table 2), a relatively large pneumatic foramen, and moderate to well-developed secondary pneumatic fossae, they also apparently fall within the Gallinuloididae. Indeed, the possibility of a reversal to an uninterrupted capital groove is supported by Mourer-Chauviré's (this volume) report of an extremely reduced humeral ridge in some of her *Quercymegapodius* specimens, i.e., the same condition found in the undescribed *Gallinuloides* sp.

Further evidence supporting our phylogenetic conclusions concerning the Gallinuloididae comes from a nearest neighbor morphometric reinvestigation of *Gallinuloides wyomingensis* (Crowe, in prep.). This analysis employs 45 of the 73 mensural osteological characters used by Crowe and Crowe (1985) and includes for comparison 147 skeletons from 98 galliform species representing all putative suprageneric taxa. The nearest neighbor analysis decisively places *G. wyomingensis* closest to the Phasianidae, more particularly with Old World perdicines, e.g., *Francolinus* spp., *Rollulus roulroul* (Scopoli 1786), *Galloperdix spadicea* (Gmelin 1789). Indeed, in this study, the first 56 nearest morphometric neighbors of *G. wyomingensis* are phasianids, 52 of which are Old World perdicines (Perdicini, *sensu* Morony et al., 1975).

With regard to qualitative features, the strong development of the scapular and sternal ends of the coracoid and the very strongly developed hypocleidium of the furcula are characteristic of the Phasianidae. Moreover, the putative cracine features of *Gallinuloides wyomingensis*, i.e., the shallow internal sternal notch and the insertion of the hind toe at the same level as the anterior toes are probably primitive features within the Galliformes (Crowe, Short, and Cracraft, in prep.).

With regard to the other relatively well-preserved Tertiary "cracid," *Procrax breviceps* Tordoff and Macdonald 1957, a morphometric investigation of this fossil (Crowe, in prep.) based on 23 of the mensural characters employed by Crowe and Crowe (1985) and the same osteological data base discussed earlier showed that 8 of its 10 nearest neighbors are phasianids and several of the "most diagnostic" cracine features are either primitive features within the Galliformes, e.g., the lack of an intercarpal tuberosity on metacarpal II, or character absences.

The remaining Palaearctic "cracids" from the Tertiary listed by Brodkorb (1964) have also been shown to belong to other gallinaceous or non-gallinaceous families (reviewed by Olson, 1985), or they are represented by single fragments of limb bones lacking sound diagnostic characters. This throws doubt on the widely held opinion that the Cracidae originated in North America (Tordoff and Macdonald, 1957; Olson, 1985) and is consistent with the hypothesis of a Gondwanaland origin for this primitive family of gallinaceous birds (Cracraft, 1973).

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NEOGENE

BIRDS

AN EARLY MIOCENE GROUND-DOVE (AVES: COLUMBIDAE) FROM FLORIDA

Jonathan J. Becker and
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ABSTRACT. A new ground dove is described from the Early Miocene (late Early Hemingfordian, 18–19 Ma) Thomas Farm local fauna, Gilchrist County, Florida. *Columbina prattae* new species, known from all major postcranial elements, is the most abundant bird at this locality, representing over 60 percent of all avian specimens. Many fossil specimens referred to this species have either medullary bone or are subadult, suggesting that members of this species were nesting in the immediate area during the formation of the fossil deposit. Vertebrate predators were probably responsible for the abundance of doves in this fossil locality.

Key words: Miocene, ground dove, Columbidae, Florida.

INTRODUCTION

The late Early Hemingfordian Thomas Farm local fauna, Gilchrist County, Florida, has produced the only large, diverse avifauna in the eastern half of North America that is more than nine million years (Ma) old (Becker, 1987). Fossil vertebrates from this locality, which include rarely preserved woodland species, have been studied since its discovery in the early 1930s and a large, diverse fauna is known, including species of bony fishes, 11 species of amphibians, 17 species of reptiles, 11 species of birds, and 27 species of mammals (Webb, 1981). Herein we describe a new species of ground dove based on more than 350 specimens from this site.

The taphonomy and paleoecology of the Thomas Farm local fauna has been intensively studied by Pratt (1986). She found that the fossiliferous sediments were deposited into a high-walled sinkhole in several different phases, including two wall collapses. The early stages of deposition randomly sampled large and small vertebrates from the surrounding habitats. With the final collapse of a wall, a cave or cave system was exposed that was frequented by bats and by mammalian and possibly avian predators. Sediments from this cave system contained abundant small mammalian remains, probably originating in mammalian carnivore scats or in cast pellets from raptorial birds.

Analysis of the mammalian fauna (Pratt, 1986) suggests that the surrounding habitat was mostly wooded, with some more open areas. Annual temperatures were warmer than at present and were probably less extreme, resulting in a more tropical environment. Annual rainfall was similar to that of present-day northern Florida and standing water was locally present.

Fossil birds described from the Thomas Farm locality include an anhinga [*Anhinga subvolans* (Brodkorb 1956)], three kites [*Promilio floridanus* (Brodkorb 1956), *P. epileus* Wetmore 1958, and *P. brodkorbi* Wetmore 1958], a cracid (*Boreortalis laesslei* Brodkorb 1954), and a phasianid (*Rhegminornis calobates* Wetmore 1958). Several other unidentified or undescribed taxa are also known, including a large anatid, an ibis, a large hawk, other galliformes, a rail, a barbet, a coraciiform, and several small passeriforms (Becker, 1987 and in prep.).

MATERIAL AND METHODS

Skeletons of the following modern species were examined (number of individuals): *Columba speciosa* (1), *C. fasciata* (1), *Streptopelia capicola* (1), *Macropygia phasianella* (1), *Turtur brehmeri* (1), *Chalcophaps indica* (1), *Ectopistes migratorius* (1), *Zenaida macroura* (10), *Z. auriculata* (2), *Z. aurita* (1), *Z. asiatica* (3), *Columbina passerina* (7), *C. minuta* (2), *C. talpacoti* (6), *C. picui* (2), *C. cruziana* (2), "*Claravis*" *pretiosa* (2), "*Metriopelia*" *ceciliae* (1), *M. melanoptera* (1), "*Scardafella*" *inca* (11), *Geotrygon mystacea* (1), *G. montana* (1), *Leptotila jamacaiensis* (1), *L. plumbeiceps* (1), *Starnoenas cyanocephala* (1), *Caloenas nicobarica* (1), *Gallicolumba criniger* (1), *Goura cristata* (1), *Treron calva* (1), *Ptilinopus perousii* (1), *Ducula zoeae* (1). These specimens are housed in the ornithological collections of Pierce Brodkorb, the American Museum of Natural History, and the National Museum of Natural History, Smithsonian Institution.

Although we list the preceding species of ground doves in several different genera, we found no diagnostic postcranial osteological characters by which to separate these genera and therefore regard *Claravis* Oberholser 1899, *Metriopelia* Bonaparte 1855, and *Scardafella* Bonaparte 1855 to be junior synonyms of *Columbina* Spix 1825. Skeletons of *Uropelia campestris* were not available, although it appears likely that *Uropelia* Bonaparte 1855 should also be included in *Columbina* based on external characters. Goodwin (1959, 1967) recognized the preceding five genera of American ground doves, but he does suggest (Goodwin, 1967) the possibility that all genera of ground doves could be included in *Columbina*.

Anatomical terminology follows that of Howard (1929) or is anglicized from Baumel et al. (1979). Measurements were taken

with Kanon dial calipers accurate to 0.05 mm and rounded to the nearest 0.1 mm.

Fossil specimens are housed in the Vertebrate Paleontology collections of the Florida Museum of Natural History (UF) or in the collections of Pierce Brodkorb (PB).

SYSTEMATIC PALEONTOLOGY

Order Columbiformes Latham 1790

Family Columbidae Illiger 1811

Subfamily Columbinae Illiger 1811

Genus *Columbina* Spix 1825

DESCRIPTION. Specimens are referable to the genus *Columbina* by the following combination of osteological characters: coracoid with sternal end with an arc-like pneumatic fossa on the medial half of the dorsal surface; ulna with a deep internal cotyla, a notched dorsal border of the olecranon process (*Geotrygon* Gosse 1847 and *Zenaida* Bonaparte 1838 similar), and the tuberculum bicipitalis very close to the ventral lip of the internal cotyla; tarsometatarsus with the medial cotyla anteroposteriorly compressed, the hypotarsus restricted to the lateral half of the bone, and the dorsal surface of trochlea IV extending dorsad (in distal view) past the level of trochlea III.

Columbina prattae new species

HOLOTYPE. Distal end of right tarsometatarsus, UF 106594.

DIAGNOSIS. *Columbina prattae* differs from all species of *Columbina* examined in having the tarsometatarsus with a more pronounced wing on trochlea II and a relatively larger distal vascular foramen.

REFERRED MATERIAL. Distal portions of 2 premaxillae, UF 96292, 106705; sterna, 21 anterior portions, UF 60972, 60986, 62074, 106402, 106408, 106409, 106483, 106529, 106530, 106571, 106706, 106714, 106719, 106789, PB 2006, 2032, 2052, 2062, 2067–2069; humeral ends of 36 right and 26 left coracoids, UF 60997, 62063, 62065–62070, 62072, 62073, 106394–106396, 106412, 106413, 106435, 106447–106450, 106454, 106467, 106468, 106472, 106474, 106475, 106498, 106559–106565, 106601–106605, 106610–106613, 106668, 106690, 106703, 106727, 106731, 106732, 106762, 106767, 106768, 106786, 106787, PB 1255, 1256, 2028, 2038, 2053, 2082, 2088, 2095; sternal ends of 6 right and 5 left coracoids, UF 106436, 106486, 106499, 106606, 106608, 106693, 106721, 106751, 106792, PB 2007, 2046; proximal ends of 19 right and 12 left scapulae, UF 60979, 60987–60990, 106443, 106452, 106463, 106465, 106491, 106492, 106539–106542, 106545, 106546, 106632–106637, 106662, 106670, 106673, 106691, 106704, 106766, 106784, 106385; 1 complete right humerus, PB 2002; proximal ends of 2 right and 2 left humeri, UF 62075, 106625, 106627, PB 2063; distal ends of 8 right and 11 left humeri, UF 60973, 62077, 62078, 96293, 96294, 106471, 106500, 106513, 106514, 106628, 106657, 106676, 106785, PB 2003, 2070, 2071, 2073, 2074, 2114; proximal ends of 3 right and 1 left ulnae, UF 106425, 106434, 106442, 106644; distal ends of 1 right and 3 left ulnae, PB 2110, 2036, 2038, 2055; 17 proximal ends of radii, UF 106441, 106462, 106490, 106551, 106615, 106664, 106696, 106697, 106701, 106734, 106756, 106757, 106796–106799, PB 2010; 14 distal end of radii, UF 106410, 106461, 106470, 106547, 106549, 106616–106620, 106398, 106699, 106711, 106748; 7 ulnare, UF 106708, 106737, 106738, PB 2056, 2058, 2100, 2101; proximal ends of 10 right and 16 left carpometacarpi, UF 60974, 62082, 62083, 106390–106392, 106404, 106411, 106464, 106520–106522, 106527, 106528, 106677, 106582, 106583, 106663, 106678, 106790; PB 1778, 2091, 2096–2099; distal ends of 17 right and 21 left carpometacarpi, UF 60998, 62084–62088, 106393, 106419, 106437, 106446, 106466, 106484, 106488, 106516–106519, 106525, 106577–106581, 106584, 106585, 106651, 106586–106589, 106667, 106669, 106723, 106726, 106771; PB 2092–2094; 10 digit 2, phalanx 1, UF 106386, 106387, 106557, 106622, 106623, 106658, 106702, 106713, 106720, 106747; 11 digit 2, phalanx 2, UF 106399, 106400, 106453, 106493, 106495, 106496, 106558, 106715–106717, 106736; 3 pollex, UF 106445, 106487, 106494; proximal ends of 6 right and 14 left femora, UF 62097, 106388, 106389, 106403, 106531–106534, 106641, 106661, 106665, 106733, 106760, 106793, 106795, PB 1254, 2009, 2025, 2027, 2049; distal ends of 5 right and 4 left femora, UF 60999, 106642, 106643, 106655, 106794, PB 2018, 2022, 2037, 2102; proximal ends of 4 right and 3 left tibiotarsi, UF 106416, 106573, 106574, 106692, 106698, PB 1253, 2008; distal ends of 9 right and 1 left tibiotarsi, UF 62089, 96267, 96295, 106444, 106536–106538, 106649, 106678, PB 2104; proximal ends of 7 right and 9 left tarsometatarsus, UF 62094, 62095, 96262, 96290, 106401, 106503, 106507, 106508, 106590, 106598, 106599, 106683, 106749, PB 2066, 2105A, 2107; shafts of 3 right and 1 left tarsometatarsi, UF 60978, 106384, 106497, 106591; distal ends of 17 right and 11 left tarsometatarsi, UF 62096, 106405, 106406, 106414, 106415, 106432, 106433, 106459, 106504–106506, 106592, 106593, 106597, 106679, 106689, 106707, 106712, 106724, 106740, 106750, 106761, 106783, PB 2005, 2105B, 2108, 2109; 4 metatarsal I, PB 2057, 2111–2113; ungual phalnax, PB 2004. Total specimens = 384; minimum number of individuals = 36, based on the humeral end of right coracoids.

TYPE LOCALITY AND HORIZON. Thomas Farm local fauna, Gilchrist County, Florida. Lower Miocene fissure fillings within the Middle Eocene Crystal River Limestone. Previously, these sediments were erroneously assigned to the Hawthorne Formation. The deposits cannot be correlated laterally by lithostratigraphy and are not suitable for radiometric dating. Based on the concurrent range zones and stage of evolution of the included fossil mammals (Tedford et al., 1987), the age of this deposit is late Early Hemingfordian (18–19 Ma). Holotype collected by Florida Museum of Natural History field party on 28 March 1978 from a lime sand (=unit 15 of Pratt, 1986; G.S. Morgan, pers. comm., 1988).

ETYMOLOGY. Named for Ann E. Pratt, in recognition of her work on the taphonomy and paleoecology of the Thomas Farm local fauna (Pratt, 1986), and who collected much of the fossil material discussed here.

DESCRIPTION. *Columbina prattae* is a medium-sized ground-dove similar to "*Claravis*" *pretiosa* (Ferrari-Perez 1886) in overall size. All species of *Columbina* are very similar osteologically, and the following comparisons are for descriptive purposes only and are not meant to suggest a close relationship within the genus. In comparison with *Columbina passerina* Linnaeus 1758 from Florida, *C. prattae* has a sternum with a longer manubrium, perforated on each side of the ventral surface by large pneumatic foramina, and by a single midline pneumatic fossa on the dorsal surface; a coracoid with a more excavated dorsal surface of the sternal end leading into a larger pneumatic fossa; a scapula with a larger acromion; a humerus with a less-pneumaticized tricipital fossa, a deeper ligamental furrow, and a more distinct brachial depression; an ulna with a deeper internal cotyla and a more deeply notched dorsal border of the olecranon; a carpometacarpus with the fovea carpalis cranialis oriented more nearly

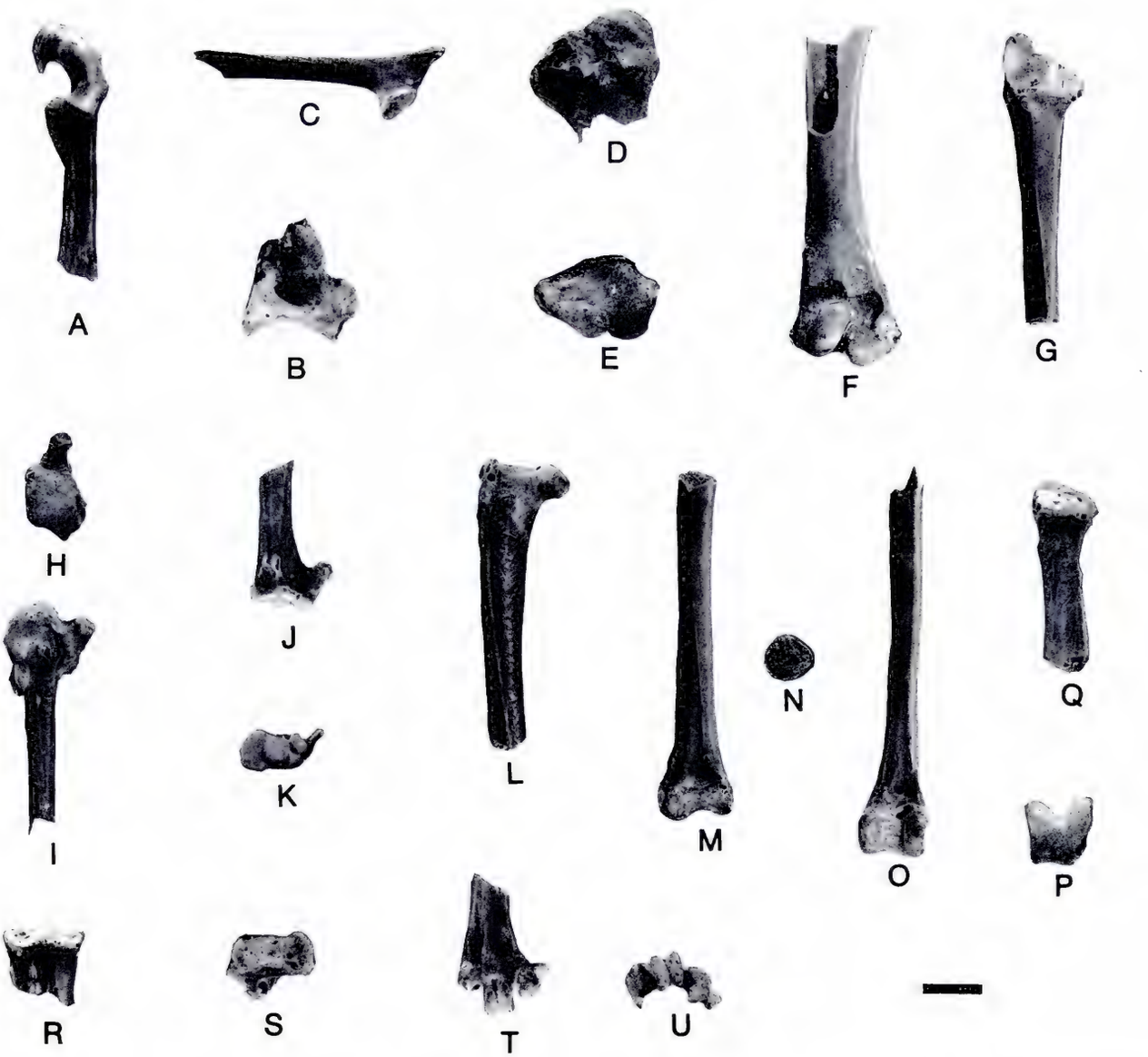

Figure 1. Holotype and referred material of *Columbina prattae* n. sp. Humeral end of right coracoid, in dorsal view (**A**), UF 106559; sternal end of right coracoid, in dorsal view (**B**), UF 106792; proximal end of right scapula, in lateral view (**C**), UF 106385; proximal end of right humerus, in caudal (anconal) view (**D**), UF 106627; distal end of right humerus, in distal end view (**E**) and in cranial (palmar) view (**F**), UF 106628; proximal end of right ulna, in cranial (palmar) view (**G**), UF 106425; proximal end of left carpometacarpus, in proximal end view (**H**) and in ventral view (**I**), UF 106583; distal end of left carpometacarpus, in dorsal view (**J**) and in distal end view (**K**), UF 62087; proximal end of right femur, in cranial view (**L**), UF 106389; distal end of left femur, in caudal view (**M**) and in cross-section of shaft showing medullary bone (**N**), UF 106794; distal end of right tibiotarsus, in cranial view (**O**) and in distal end view (**P**), UF 96267; proximal end of right tibiotarsus, in caudal view (**Q**), UF 106574; proximal end of left tarsometatarsus in dorsal view (**R**) and in distal end view (**S**), UF 96290; and distal end of right tarsometatarsus, in dorsal view (**T**) and in distal end view (**U**), UF 106594, holotype. Magnification is approximately 2.5×. Scale bar = 3 mm.

parallel to the long axis of the shaft; a femur with a more pronounced crista supracondylaris medialis and a deeper fossa poplitea; a tibiotarsus with external condyle more nearly circular in lateral view; and a tarsometatarsus with a deeper parahypotarsalis medialis fossa. Because complete skeletal elements of *Columbina prattae* are lacking, comparisons of total lengths and relative limb proportions cannot be made. Although preliminary faunal lists published previously listed two species of dove being present in this local fauna (e.g., Webb, 1981), we regard all columbid specimens available to us from the Thomas Farm locality to represent a single species.

MEASUREMENTS. See Table 1.

DISCUSSION

Very few Tertiary species of doves are known. Milne-Edwards (1869) described *Columba calcaria* from a left humerus of Aquitanian age collected between Saint-Gérand-le-Puy and Langy,

Table 1. Measurements of skeletal elements of *Columbina prattae* n. sp. as follows: Coracoid: least depth of head (D–HEAD); scapula: length from tip of acromion through ventral edge of glenoid facet (ACR–GLN); width of glenoid facet (W–GLN); humerus: transverse width of distal end (W–DIST); depth of distal end, measured through external condyle (D–DIST); ulna: transverse width of proximal articular surface (W–PROX); length from tip of olecranon to tip of external cotyla (D–LENGTH); carpometacarpus: transverse width of carpal facet (W–CARPAL); depth of proximal end from tip of metacarpal I through carpal trochlea (D–PROX); greatest depth of distal end measured across dorsal edge of facet for digit II (D–DIST); transverse width of distal end (W–DIST); femur: transverse width of proximal end (W–PROX); depth of femoral head (D–HEAD); transverse width of distal end (W–DIST); depth of medial condyle (D–MCON); tibiotarsus: transverse width of distal end measured across cranial portion of condyles (W–DIST–CR); depth of lateral condyle (D–LCON); tarsometatarsus: transverse width of proximal end, measured across dorsal surface (W–PROX); transverse width of distal end (W–DIST); width of trochlea III (W–TRIII); depth of trochlea III (D–TRIII).

Measurement	Mean	SD	n	Min.–Max.
Coracoid				
D–HEAD	2.35	0.16	31	2.1–2.7
Scapula				
ACR–GLN	5.18	0.32	14	4.6–5.6
W–GLN	2.13	0.13	23	1.8–2.3
Humerus				
W–DIST	6.04	0.44	9	5.2–6.7
D–DIST	3.71	0.22	9	3.3–3.9
Ulna				
W–PROX	3.6	0.26	3	3.4–3.9
D–LENGTH	4.63	0.51	3	3.0–5.2
Carpometacarpus				
W–CARPAL	2.48	0.16	15	2.1–2.6
D–PROX	5.15	0.29	11	4.7–5.6
D–DIST	2.04	0.12	21	1.8–2.2
W–DIST	3.17	0.17	21	2.9–3.5
Femur				
W–PROX	4.33	0.11	7	4.1–4.4
D–HEAD	1.83	0.13	8	1.7–2.0
W–DIST	4.0	—	2	3.9–4.1
D–MCON	3.2	—	2	3.2–3.2
Tibiotarsus				
W–DIST–CR	3.38	0.11	5	3.2–3.5
D–LCON	3.43	0.06	3	3.4–3.5
Tarsometatarsus				
W–PROX	3.85	0.20	10	3.5–4.1
W–DIST	4.18	0.21	4	4.0–4.4
W–TRIII	1.41	0.11	17	1.2–1.6
D–TRIII	1.64	0.10	18	1.5–1.9

Allier, France. Later, Lambrecht (1933) erected a new genus, *Gerandia*, for this species, partly in response to Lydekker's (1891) comment that the genus *Columba* would have to be used in a wider sense if it included some of the fossil forms then placed in it. The precise systematic relationships of this monotypic fossil genus are still uncertain (Olson, 1985).

Columba omnisanctorum Ballman 1976 was based on a tarsometatarsus, coracoid, humerus, and ulna that were similar in size to *Columba oenas* Linnaeus 1758 and of "modern" aspect (Ballmann, 1976:43). This species is from Upper Miocene fissure fillings on the Gargano Peninsula, Italy, that are considered to be somewhat later in time than those of La Grive–St. Alban, France (Ballmann, 1976). The only Neogene species of columbid previously described from North America is *Zenaida prior* (Brodkorb 1969) from the Blancan Rexroad local fauna, Kansas, which is very close to the living *Zenaida macroura* (Linnaeus 1758). All three of these previously described fossil species are larger than *Columbina prattae*.

All other extinct species of Columbiformes that have been described are from upper Quaternary deposits on islands in the Indo-Pacific and South Atlantic and from Cenozoic deposits in Australia (Brodkorb, 1971; Olson, 1975; van Tets and Rich, 1980; Rich and van Tets, 1982; Balouet and Olson, 1987; Balouet and Olson, 1989). Modern species of doves have also been reported from many fossil and subfossil deposits on islands in the Caribbean and Pacific Oceans (e.g., Olson and Hilgartner, 1982; Steadman et al., 1984; Steadman, 1985).

Columbina prattae is by far the most abundant bird in the Thomas Farm local fauna, making up over 60 percent of all avian fossils recovered. Its bones are most abundant in the lime sand representing cave sediments in the later depositional phases (unit 15 of Pratt, 1986). Over 85 percent of the dove specimens with detailed microstratigraphic information are from this unit.

Some specimens represent individuals in breeding condition, as shown by the presence of medullary bone (Fig. 1N) (Hodges, 1974:289; Taylor et al., 1971:627), and many other bones have the porous appearance of subadult individuals. The presence of these bones provides strong evidence that *Columbina prattae* was nesting in the immediate area during formation of the fossil deposit.

Several possibilities could explain the unusual abundance of skeletal elements of *Columbina prattae* at this fossil locality. Because doves are most common in sediments that produce abundant remains of small mammals interpreted as a coprocenosis, the most likely explanation is that doves, including females and young, were prey for one or more of the mammalian or avian predators. The determination of which vertebrate predator was responsible may not be possible if the fossil community represented at Thomas Farm was functioning in a manner similar to that of modern communities. Jaksić and Delibes (1987) demonstrate that modern vertebrate predators can have substantial dietary overlap, even when they are members of diverse taxonomic groups. Other, less likely, possibilities are that this species of dove was using the sinkhole/cave system as a nesting site or as a water source.

Because of the lack of modern comparative skeletons, comparisons could not be made with four extant species of ground-doves [*Columbina cyanopis* (Pelzeln 1870), *C. godefrida* (Temminck 1811), *C. morenoi* (Sharpe 1902), and *Uropelia campestris* (Spix 1825)]. Comparisons were further hampered by the lack of unbroken skeletal elements of the fossil species and by the lack of a modern osteological revision of the Columbidae. These deficiencies do not affect the validity of *Columbina prattae*, but they do prevent resolution of the phylogenetic relationships within the genus *Columbina*.

The lack of complete skeletal elements of *Columbina prattae* reflects the collecting techniques necessitated by the high clay content in the sediments rather than taphonomic processes. Fossiliferous sediment is washed through fine-mesh screens and thoroughly dried. This process is repeated several times and the

expansion and contraction of the clay caused by this procedure splinters nearly all of the less robust skeletal elements.

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REVISION OF *DROMAIUS GIDJU* PATTERSON AND RICH 1987 FROM RIVERSLEIGH, NORTHWESTERN QUEENSLAND, AUSTRALIA, WITH A REASSESSMENT OF ITS GENERIC POSITION

Walter E. Boles

ABSTRACT. *Dromaius gidju* Patterson and Rich 1987, from the Miocene Kutjamarpu local fauna of central Australia, was described on the basis of associated hindlimb elements. New hindlimb material from the type locality and from Oligocene/Miocene deposits in Riversleigh, northwestern Queensland, are referred to this taxon. Tibiotarsal and tarsometatarsal remains of *D. gidju* are more similar to those of emus than those of cassowaries, whereas the femora are more similar to femora of cassowaries. All hindlimb elements of *D. gidju* show some affinity to both cassowaries and emus. The combination of hindlimb characters indicates an earlier stage in the development of increased cursoriality, so I propose a new genus for this taxon, *Emuarius,* which is interpreted to be nearer the mutual ancestor of the emu and cassowary lineages than any other described form.

Key words: fossil, emu, cassowary, Casuariidae, *Dromaius, Casuarius, Emuarius,* Riversleigh, Australia.

INTRODUCTION

Emus and cassowaries (Casuariidae: Casuariiformes) comprise one of the most distinctive and characteristic elements of the Australo-Papuan avifauna (Fig. 1). I follow the practice of Patterson and Rich (1987), Rich et al. (1988), and others of considering *Casuarius* Brisson 1760 and *Dromaius* Vieillot 1816 as representing two subfamilies within the Casuariidae, rather than as comprising separate families. Emus (*Dromaius;* Dromaiinae) are represented by a single living species, *D. novaehollandiae* (Latham 1790), which is restricted to the Australian mainland. Two dwarf, insular species have become extinct in recent times: *D. ater* Vieillot 1817 [=*D. minor* Spencer 1906 *auct.*] on King Island, in Bass Strait between Tasmania and the mainland, and *D. baudinianus* Parker 1984, on Kangaroo Island, off the South Australian coast (Parker, 1984). The taxonomic status of the extinct Tasmanian population of *D. novaehollandiae diemenensis* Le Söuef 1907 is unresolved. Cassowaries (*Casuarius;* Casuariinae) are represented by three extant species: the Southern or Double-wattled Cassowary, *C. casuarius* Linnaeus 1758 (northeastern Australia, New Guinea, Seram—introduced?), Single-wattled Cassowary, *C. unappendiculatus* Blyth 1860 (New Guinea), and Bennett's or Dwarf Cassowary, *C. bennetti* Gould 1857 (New Guinea, New Britain—introduced?) (Mayr, 1979). Despite forming a distinctive and endemic or near endemic part of the Australo-Papuan avifauna, the family Casuariidae has had, until recently, only a small representation in the fossil record, thus presenting virtually no clues about the divergence of the subfamilies.

Based on fossil and Recent material, the Casuariinae and Dromaiinae represent graviportal and cursorial birds, respectively, with concomitant preferences for more densely vegetated and more open habitats. The differences listed in Table 1, taken from Patterson and Rich (1987) and Rich et al. (1988), distinguish cassowaries from emus for the elements available. The intermediate, mosaic nature of the material described in this paper blurs some of these distinctions, with some elements exhibiting more features characteristic of the Casuariinae, whereas others are more similar to those of the Dromaiinae.

The recently described *Dromaius gidju* Patterson and Rich 1987 from central Australia has some characters that indicate it was less cursorial than other emus, suggesting that it may have been close to a mutual emu–cassowary ancestor. Patterson and Rich (1987:99) placed *Dromaius gidju* with the emus on the basis of available material, but they noted that "... as our records of this form increase, there may be sufficient reason to separate it from both genera within this family as an early, quite unspecialized form." New finds from Riversleigh, northwestern Queensland, extend the known geographic range of *D. gidju* and permit a reassessment of the generic placement of this taxon.

MATERIALS AND METHODS

Names of species taxa for Recent *Casuarius* and *Dromaius* follow Mayr (1979), except for the use of *D. ater* as the name for the King Island population and recognition of the distinction of *D. baudinianus,* which follow Parker (1984). Measurements were made with vernier calipers accurate to 0.05 mm and rounded to the nearest 0.1 mm. Terminology primarily follows that of Howard (1929, 1980). The holotype of *D. gidju* is in the South Australian Museum. Other material referred to this taxon herein is currently held in the collections of the Vertebrate Paleontology Laboratory, University of New South Wales, but it will be transferred to either the Australian Museum or the Queensland Museum. Initial citations of fossil material give the registration numbers of both the Vertebrate Paleontology Laboratory and respective museum; thereafter, only the museum number is cited. The following abbreviations are used: AM, Australian Museum; AR, Vertebrate Palaeontology Laboratory,

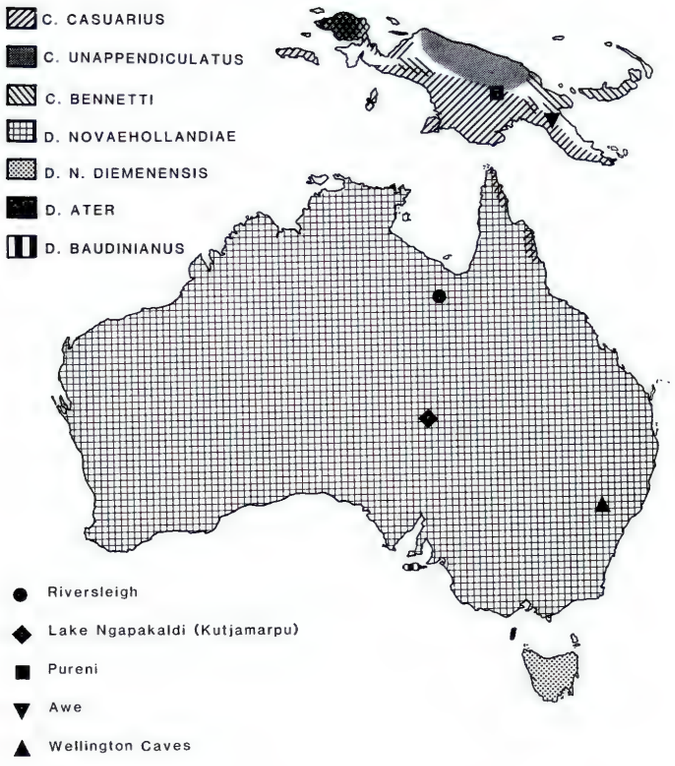

Figure 1. Distribution of Recent species of *Dromaius* and *Casuarius* and casuariid fossil-bearing localities mentioned in the text.

University of New South Wales; CPC, Commonwealth Palaeontological Collections, Bureau of Mineral Resources, Canberra; QM, Queensland Museum; SAM, South Australian Museum; and UCMP, University of California, Museum of Paleontology, Berkeley.

FOSSIL HISTORY

The fossil histories of the emus and cassowaries have recently been reviewed by Patterson and Rich (1987) and Rich et al. (1988), respectively, thus necessitating only brief synopses here (see also Rich and Baird, 1986).

DROMAIINAE. Of the nominal forms of emus known from fossil remains, Patterson and Rich (1987) maintained two. After eliminating several fossils incorrectly assigned to the subfamily Dromaiinae, these authors recognized *Dromaius ocypus* Miller 1963 from the Pliocene Palankarinna local fauna of the Lake Eyre basin, South Australia, and referred all other determinable mainland material, including *D. patricius* De Vis 1888 and *D. gracilipes* De Vis 1892, to the modern *D. novaehollandiae.* They noted that there may have been greater variability in body size in Pleistocene emus than at present, but confirmation awaits further material of both fossil and Recent birds.

As part of their review, Patterson and Rich (1987) described *Dromaius gidju* from the Miocene Kutjamarpu local fauna of northern South Australia. From a partial left leg consisting of the distal end of a tibiotarsus, articulating proximal end of the tarsometatarsus, and a complete pes, they recognized that this form was smaller and more gracile than other emus. It had a shorter tarsometatarsus, and both this bone and the phalanges were less mediolaterally compressed than in other members of the genus. Additionally, digits II and IV were less reduced. These authors interpreted this as an indication that *D. gidju* was the least cursorial member of the genus.

A small emu from the Late Miocene is represented in the Alcoota local fauna, Northern Territory (Patterson and Rich, 1987). It is similar in size to *Dromaius gidju* and possibly referable to that taxon, but because the remains are scanty (just fragmentary tarsometatarsi and phalanges) Patterson and Rich (1987) assigned it to *Dromaius* sp. indet. pending discovery of additional material.

CASUARIINAE. Lydekker (1891) reported a small cassowary from the Pleistocene of New South Wales based on the distal end of a right tibiotarsus; it was subsequently named *Casuarius lydekkeri* Rothschild 1911. This fossil was presumed to have come from the Wellington Caves. However, the manner of preservation is not matched by other material from these deposits, and several workers have expressed doubt about the presumed locality (Rich et al., 1988).

Plane (1967) reported three phalanges from the Pliocene Awe local fauna, Papua New Guinea, without referring them to a species. Although closest to *Casuarius bennetti* among living species, there were sufficient differences in the shape and proportions of the bones to doubt that they were from this species.

Rich et al. (1988) described a pygmy cassowary from Pleistocene bog deposits at Pureni, Papua New Guinea, that cannot be separated from *Casuarius lydekkeri* on the basis of the distal end of the tibiotarsus, the only shared element. Consequently, those authors referred all the Pureni material to this species, noting that, although it shares several features with *C. bennetti,* in other ways it more closely resembles *C. casuarius.* Lack of common elements precluded comparison with the Awe cassowary.

NEW CASUARIID MATERIAL. New material from Riversleigh includes fragments of lower limb bones (femur, tibiotarsus, tarsometatarsus), a scapulocoracoid, and a partial maxilla, all referred to *Dromaius gidju.* A small femur referred herein to this family was collected from the Leaf Locality, the type locality for *D. gidju.* This new material and its bearing on the relationships of *D. gidju* form the subject of this paper.

GEOGRAPHIC AND GEOLOGICAL SETTING

The material described as *Dromaius gidju,* and an additional bone reported herein, came from the Leaf Locality (UCMP V-6213), a site on the eastern shore of Lake Ngapakaldi in the eastern Lake Eyre sub-basin, South Australia. The Leaf Locality faunal assemblage including this taxon is the Kutjamarpu local fauna. The age of this fauna is suggested by its diprotodontid marsupials, whose closest affinities lie with those from the Riversleigh and Bullock Creek local faunas. The latter are understood to be between Late Oligocene and Middle Miocene in age (Archer et al., 1989).

The Riversleigh deposits are located on Riversleigh Station, approximately 200 km north of Mount Isa, northwestern Queensland. Only one of the sedimentary units has been given a formal name, the Carl Creek Limestone (Tedford, 1967), which is currently interpreted to be Upper Oligocene to Middle Miocene (Archer et al., 1989). It is probably similar in age to the Kutjamarpu local fauna (Archer et al., 1989). Many Tertiary and Quaternary local faunas have been discovered at Riversleigh, the names of a number of which have been established in the literature. Stratigraphic relationships among these faunas are starting to become clear (Archer et al., 1989), but these, as well as their interpreted ages, are regarded as tentative.

Table 1. Comparison of some diagnostic characters of the hindlimbs of *Casuarius, Dromaius,* and *Emuarius.*

Character	*Casuarius*	*Dromaius*	*Emuarius*
Maxilla			
Shape	Narrow, pointed	Broad, rounded, flattened	Broad, rounded, flattened
Femur			
Pneumatic foramen proximally and posteriorly	Absent	Present	Absent
Diameter of head relative to minimum diameter of shaft at proximodistal midpoint	Diameter of head less	Diameters of head and shaft subequal	Diameter of head less
Relative proximal extension of internal and external condyles (anterior view)	Nearly equal	External decidedly greater	External moderately greater
Border of internal condyle (medial view)	Angular, triangular	Semicircular, smoothly rounded	Angular, triangular
Relative depth of condyles (distal view)	Nearly equal	External noticeably deeper	External moderately deeper
Shaft (posterior view)	Elongate, slender, sides nearly parallel	Stouter, decidedly curved medially	Elongate, slender, sides nearly parallel
Shaft (lateral view)	Curved, decidedly concave posteriorly	More or less straight	Curved, decidedly concave posteriorly
Tibiotarsus			
External condyle (lateral view)	Rounded	Distally flattened	Rounded
Small ridge between anterior intercondylar fossa and dorsal and lateral of midline	Absent	Present	Present
Tarsometatarsus			
Relative lengths of tibiotarsus and tarsometatarsus	Tibiotarsus decidedly longer	Subequal	Not known
Intercotylar prominence	High, convex	Low, tending flat	High, convex
Medial border of internal cotyla	Rounded, tilted sharply laterad posterior to anteroposterior midpoint	More flattened	More flattened
Relative sizes of trochleae II and IV, distally	Nearly equal	Trochlea II decidedly smaller	Trochlea II somewhat smaller
Distal foramen penetrating bone anteroposteriad	Absent	Present	Absent
Proximal foramen penetrating bone anteroposteriad	Present but roofed over	Often present	Present
Pes			
Divergence of condyles of phalanges plantarly	Moderately diverging	Greatly diverging	Greatly diverging
Intercondylar fossa (distal view)	More deeply notched and more V-shaped	Only slightly notched in step-shaped fashion dorsally	Only slightly notched in step-shaped fashion dorsally
Digit with longest ungual phalanx	II	III	II

Three of the local faunas yielding material of *Dromaius gidju* come from Godthelp Hill (Camel Sputum and Upper Site local faunas) and Hal's Hill (White Hunter local fauna), interpreted to be ?Early to Middle Miocene in age. The fourth Riversleigh source of *D. gidju* is the Dwornamor local fauna from the Gag Plateau, considered to be ?Middle Miocene in age.

Other faunal similarities exist between the various Riversleigh local faunas and the Kutjamarpu local fauna, including a species of lungfish, potoroids (e.g., *Wakiewakie lawsoni* Woodburne 1984), thylacoleonids (a species of *Wakaleo* Clemens and Plane 1974), and diprotodontids (e.g., *Neohelos tirarensis* Stirton 1967) (Archer et al., 1989).

SYSTEMATIC PALEONTOLOGY

It is necessary to determine that material referred to *Dromaius gidju* belongs to the Casuariidae and not to the Dromornithidae, another group of large, flightless, terrestrial birds, remains of at least two species of which also have been recovered from the Riversleigh deposits. Only a selection of characters for the avail-

able elements of *D. gidju* is presented here; for a more extensive review of differences, see Rich (1979, 1980), from which these characters are taken. The condition in the casuariids is given first (followed by that of dromornithids in parentheses).

Maxilla. Dorsoventrally flattened (deep, sharply angled, culmen strongly arched).

Scapulocoracoid. In anterior view, large process extending mediad of glenoid facet (process absent).

Femur. Posterior margin of proximal articular surface highly concave anteriorly (nearly straight or only slightly indented); in lateral view, dorsal margin of external condyle highly concave proximally (nearly straight or only slightly concave); popliteal area moderately wide (broad); in posterior view, internal condyle subequal to or narrower than external condyle (broader); in medial view, shaft near distal end straight to slightly concave internally (highly concave).

Tibiotarsus. Supratendinal bridge absent (present); tendinal canal displaced far mediad of midline (centrally located); ridge extending laterad from distal border of supratendinal bridge area laterad of tendinal canal present (absent); excavation near anterior end of external condyle present (absent); low knob extending far laterad near anteroposterior midpoint of external condyle present (absent).

Tarsometatarsus. In proximal view, hypotarsus narrow, centrally located, triangular (broad, rectangular); calcaneal canals absent (present); in proximal view, internal border of proximal end not ridged (ridged); posterior shaft surface deeply grooved (ungrooved); distal margin of trochlea IV grooved (ungrooved); depth of trochleae moderate (deep); medial and lateral margins of trochlea III parallel (convergent posteriorly).

Pes. Phalangeal count of digits II–IV 3–4–5 (3–4–4); proximal articular surface deeply biconcave (flattened, slightly concave proximally); ungual phalanx claw-like (hoof or spade-like, broad, shallow).

The Kutjamarpu and Riversleigh femora exhibit a preponderance of similarities to those of cassowaries, although they also share some features with emus. Conversely, the holotypic material and new tibiotarsi and tarsometatarsi are more like those of emus but, again, display some features associated with cassowaries. The partial maxilla is definitely more similar to that of emus. The scapulocoracoid, while more like that of emus than cassowaries, has its own distinctive features.

Order Casuariiformes Sclater 1880

Family Casuariidae Kaup 1847

Subfamily Dromaiinae Gray 1870

DESCRIPTION. Maxilla broad, rounded, flattened. Skull lacking bony crest. Femur, in anterior view, external condyle with moderately to decidedly greater proximal extension than internal condyle. Tibiotarsus, small ridge above anterior intercotylar fossa running dorsal and lateral of midline. Tarsometatarsus, medial border of internal cotyla flattened; distally, trochlea II decidedly narrower than trochlea IV; relative lengths of tibiotarsus and tarsometatarsus subequal. Pes, condyles of phalanges tending greatly divergent plantarly; in distal view, intercondylar fossa slightly notched in step-shaped fashion dorsally; ungual phalanx of digit II not spike-like.

Emuarius new genus

TYPE SPECIES. *Dromaius gidju* Patterson and Rich 1987.

DIAGNOSIS. *Emuarius* can be distinguished from *Dromaius* by the following combination of characters: **scapulocoracoid,** shaft of coracoid mediad of glenoid facet and blade of scapula rotated dorsolaterad; glenoid facet directed dorsolaterad; **femur,** pneumatic foramen proximally and posteriorly absent; diameter of head less than minimum diameter of shaft at its proximodistal midpoint; in posterior view, shaft elongate, slender with nearly parallel sides; in lateral view, shaft curved, decidedly concave posteriorly; **tibiotarsus,** in lateral view, external condyle rounded; **tarsometatarsus,** intercotylar prominence high, convex; distal foramen completely penetrating tarsometatarsus anteroposteriorly proximad to trochlea III and IV, proximal foramen absent; **pes,** digit II with longest ungual phalanx.

ETYMOLOGY. *Emuarius* is formed from the combination of "Emu" and "*Casuarius*," in allusion to its intermediate position between these taxa. The roots of the word are *emu,* the English name of the genus *Dromaius,* which comes from the Portuguese word "ema," meaning crane, and often other large birds, itself derived from the Arabic word "Na^{-c}amah" (naema) for Ostrich, *Struthio camelus* Linnaeus 1758; and *arius* from "weri," a Papuan word meaning head (Macdonald, 1986). The gender is masculine.

Emuarius gidju (Patterson and Rich 1987) new combination

Figures 2–7

HOLOTYPE. SAM P26779, associated left leg consisting of distal tibiotarsus, proximal tarsometatarsus and complete pes.

EMENDED DIAGNOSIS. As for genus.

TYPE LOCALITY AND HORIZON. Leaf Locality (UCMP V-6213), from unnamed deposits in the Wipajiri Formation, Lake Ngapakaldi, Etadunna Station, eastern Lake Eyre basin, South Australia.

TYPE LOCAL FAUNA AND AGE. Kutjamarpu local fauna, Late Oligocene/Early Miocene (Archer et al., 1989; previously Middle Miocene *fide* Woodburne et al., 1985).

REFERRED MATERIAL, LOCAL FAUNAS, AND AGES.

1. Kutjamarpu local fauna (Leaf Locality): AM F78585 (AR 3215), complete right femur with abrasion to head and trochanter.

2. White Hunter local fauna (White Hunter Site), Hal's Hill, Riversleigh, Queensland; ?Early to Middle Miocene: QM F16827 (AR 10130), distal end of right tibiotarsus with damaged internal condyle.

3. Camel Sputum local fauna (Camel Sputum Site), Godthelp Hill, Riversleigh, Queensland; ?Early to Middle Miocene: QM F16828 (AR 12795), femur with complete shaft and damage to the head, trochanter, and external and internal condyles; QM F16829 (AR 13359), distal end of right femur with damaged condyles and posterior surface; AM F78586 (AR 10851), distal right tibiotarsus lacking distal tip.

4. Upper Site local fauna (Upper Site), Godthelp Hill, Riversleigh, Queensland; ?Early to Middle Miocene: QM F16830 (AR 14263), tip of maxilla with little damage; QM F16831 (AR 12804), midshaft of right scapulocoracoid, including glenoid facet, but lacking sternal end of coracoid and most of scapula.

5. Dwornamor local fauna (Gag Site), Gag Plateau, Riversleigh, Queensland; ?Middle Miocene: QM F16832 (AR 3883), distal end of right femur with damaged condyles and intercondylar fossa; AM F78587 (AR 5233), distal end of left tarsometatarsus with some damage to trochleae II and III.

MEASUREMENTS. See Tables 2–6.

DESCRIPTION. Maxilla. As preserved, greatest width 11

Figure 2. Right femora of casuariids. Left to right: *Casuarius casuarius* (QM O20695), *C. bennetti* (AM O42539), *Emuarius gidju* (AM F78585), *Dromaius novaehollandiae* (AM S1515), *D. ater* (AM F16463), 0.4×. **A,** posterior view; **B,** lateral view.

Figure 3. Right femora of casuariids. Left to right: *Casuarius casuarius* (QM O20695), *C. bennetti* (AM O42539), *Emuarius gidju* (AM F78585), *Dromaius novaehollandiae* (AM S1515), *D. ater* (AM F16463), 0.4×. **A,** anterior view; **B,** medial view.

Table 2. Measurements (mm) of femora of *Emuarius gidju*.

	AM F78585	QM F16832	QM F16828
Proximal end			
1. Maximum width	>39.2	—	—
2. Depth of head	16.7±	—	—
3. Maximum depth, proximal end	40.2±	—	—
Distal end			
4. Maximum width across condyles	38.0±	43.6	—
5. Maximum width, internal condyle, posterior surface	18.1±	20.3	—
6. Maximum depth, internal condyle	—	—	40.0
7. Maximum width, external condyle, posterior surface	18.8±	—	—
8. Maximum depth, external condyle	>40.2	—	—
9. Distal width, rotular groove	8.1±	—	—
10. Minimum shaft width	20.3	—	21.0
11. Minimum shaft depth	21.0	—	19.0
12. Total length of femur (trochanter to distal end external condyle)	>194.0	—	—
13. Total length of femur (head to distal end internal condyle)	>181.8	—	—

mm; length at midline symphysis 10 mm. Tip rounded; entire surface dorsoventrally flattened, curving gradually along culmen to tip. Upper surface convex, separated into two lateral sections divided by central ridge; lateral sections slightly convex, curving into a groove along central ridge; edges of central ridge subparallel to slightly diverging distad (minor damage prevents accurate assessment). Undersurface angularly concave.

Both surfaces, particularly along the border, are highly porous, more so than in the maxillae of adult emus. The size and porosity suggest that the specimen came from a very young bird. In shape, it is much broader than the narrow, pointed maxilla of *Casuarius*, agreeing in overall width with *Dromaius*. The maxillary tip of *Emuarius* is rounder, less triangular than that of similarly sized *D. novaehollandiae*.

Parkes and Clark (1966) drew attention to a configuration of the rhamphotheca found in ratites and tinamous (Tinamidae) but not in neognathous birds. In the former birds, the rhamphotheca appears to be divided into sections, with a median nail-like region separated by longitudinal grooves from bordering lateral pieces (called segments by those authors). Cracraft (1974) considered this to be one of the three derived characters that defined the ratites and tinamous as a natural group. Olson (1985) noted that these grooves were also present on the underlying bones of the maxilla. The presence of these structures permits the identification of the maxillary fragment from Riversleigh as a ratite. Because I believe only one small ratite was present in the Riversleigh and Kutjamarpu faunas (see Discussion), I have referred this maxilla to *Emuarius gidju*, rather than to *Dromaius* sp. indet.

Scapulocoracoid. Blade of sternal end flattened, posteriorly slightly concave; narrowest sternad of glenoid facet. Midshaft of coracoid deep, arched anteriad, becoming increasingly arched medial to glenoid facet, with numerous small ridges. Slight ridge along top of arched anterior midline of midshaft of coracoid running into elongate knob at obtuse angle; knob directed toward middle of glenoid facet. Shaft humerad of coracoid blade rotated dorsolaterad, including small remaining portion of scapular blade forward of glenoid facet. Glenoid facet oriented dorsolaterad.

This element shows the greatest divergence from either living genus. The shaft medial to the glenoid facet is deeper, more arched, and more heavily ridged, and the orientation of the glenoid facet is directed more dorsad. The width of the coracoid shaft sternad of the glenoid facet most resembles *Dromaius*. This element is similar to that of *Casuarius* in having a knob medial to the glenoid facet on the anterior surface, though in *Emuarius* it is more humerad relative to the facet. Because of these differences and for the reasons given for the maxilla, I have referred this scapulocoracoid to *Emuarius gidju*, rather than to species indeterminate in either *Dromaius* or *Casuarius*.

Femur. Lateral face of proximal end with strongly defined muscle scars. Proximal extent of trochanter greater than that of head but damage prevents assessment of total extent. Obturator ridge oriented anterolaterad. Posterior intermuscular line running along midline of shaft parallel to edges; about one-third of shaft length distal to proximal end another ridge angles proximomediad from posterior intermuscular line to base of head. In anterior view, external condyle with moderately greater proximal extension than internal condyle. Distal border of internal condyle in medial view triangular in shape; proximal margin smoothly curved into shaft.

If examined in isolation, the femur of *Emuarius gidju* would be considered that of a cassowary. It differs from that of *Dromaius* in most of the characters given by Patterson and Rich (1987) and Rich et al. (1988) (Table 1). In two characters of the condyles (relative proximal extension in anterior view and relative depth in distal view), the conditions are intermediate between those in *Casuarius* and *Dromaius*.

The Kutjamarpu femur is somewhat longer than the femora of the dwarf emus, but the shaft is both actually and proportionally thinner. The proximal end of *Emuarius gidju*, in both anterior and lateral views, is narrower than those of the small species of *Dromaius*. The distal end, so far as the damage to *E. gidju* material permits assessment, is narrower in anterior view.

Damage to the Riversleigh femur (QM F16828) prevents a comparison with the most important features of the comparable Kutjamarpu element, though minor differences can be detected in the shaft. The Riversleigh bone is longer, based on comparable points on the most protruding point of the internal condyle and

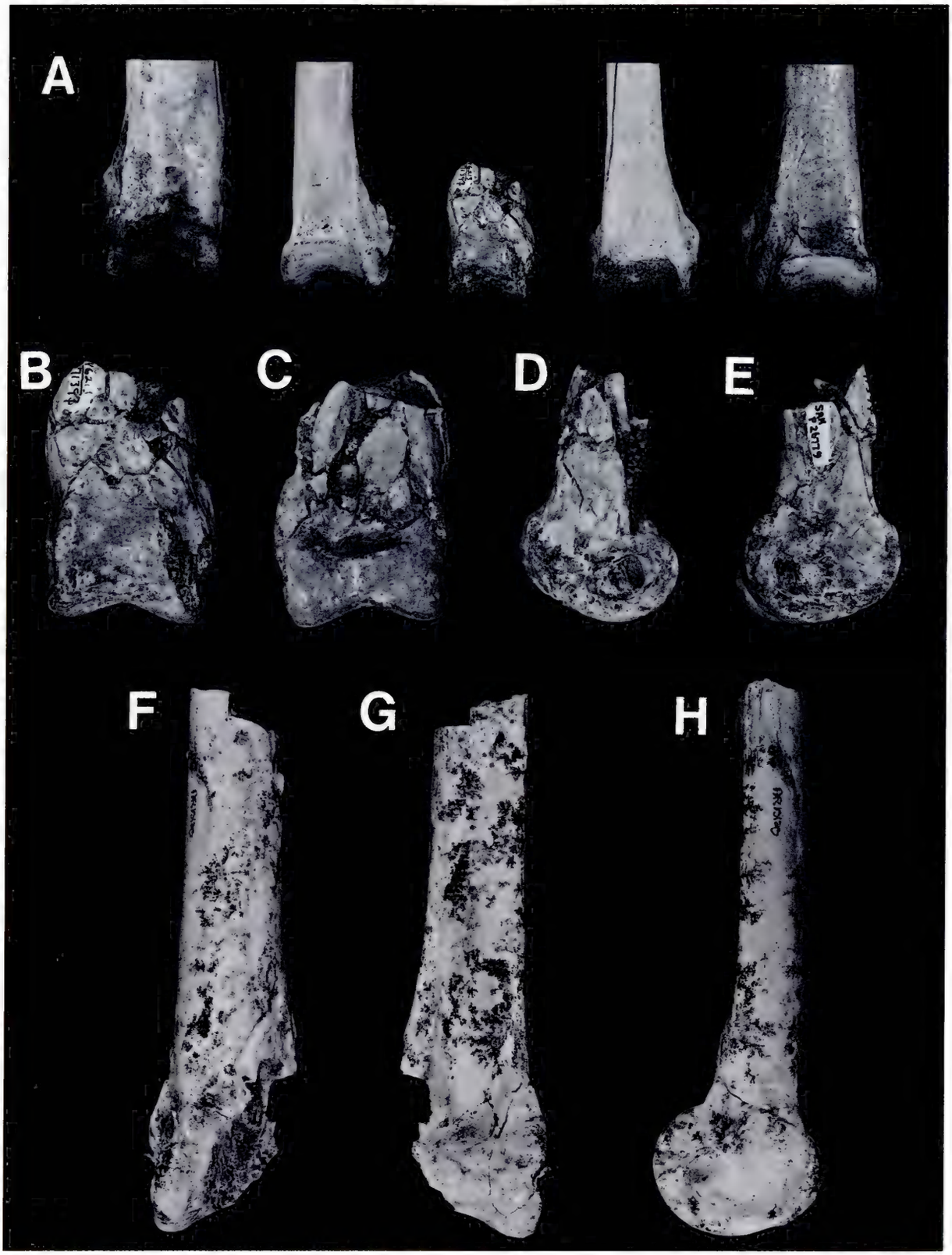

Figure 4. **A.** Left tibiotarsi of casuariids, distal end, posterior view, 0.4×. Left to right: *Casuarius casuarius* (QM O3434), *C. bennetti* (AM O42539), *Emuarius gidju* (SAM P26779), *Dromaius novaehollandiae* (AM S1515), *D. ater* (AM F15560). **B–E.** Left distal tibiotarsus of *E. gidju*, SAM P26779 (holotype), Kutjamarpu local fauna, 1×, in (**B**) posterior, (**C**) anterior, (**D**) medial, and (**E**) lateral views. **F–H.** Right distal tibiotarsus, QM F16827, White Hunter local fauna, 1×, in (**F**) posterior, (**G**) anterior, and (**H**) lateral views.

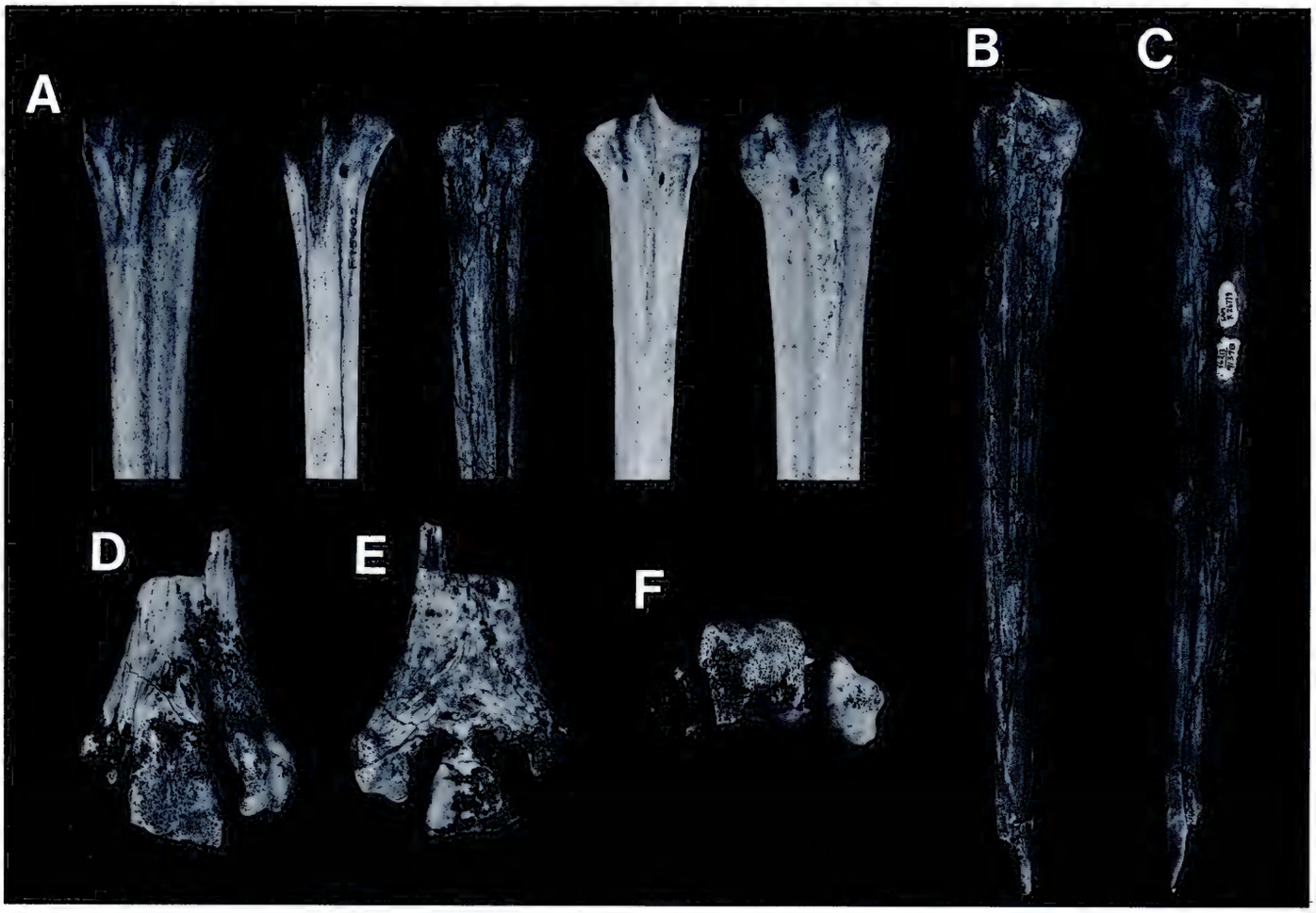

Figure 5. **A.** Left tarsometatarsi of casuariids, proximal end, posterior view, 0.6×. Left to right: *Dromaius novaehollandiae* (AM S1515), *D. ater* (AM F15602), *Emuarius gidju* (SAM P26779), *Casuarius bennetti* (AM O42539), *C. casuarius* (QM O20698). **B, C.** Left proximal tarsometatarsus of *E. gidju*, SAM P26779 (holotype), Kutjamarpu local fauna, 0.6×, in (**B**) posterior and (**C**) anterior views. **D–F.** Left distal tarsometatarsus of *E. gidju*, AM F78587, Dwornamor local fauna, 1×, in (**D**) anterior, (**E**) posterior, and (**F**) distal views.

the same muscle scar on the lateral face of the proximal end. The shaft of the Kutjamarpu femur flares somewhat more abruptly into the obturator ridge.

These femora differ from those of modern cassowaries by being markedly smaller than even the smallest of extant species, *Casuarius bennetti*, and decidedly more gracile than all living cassowaries. They differ from the femur of *C. lydekkeri* from Pureni (CPC F23025), the other extinct pygmy form, by a combination of characters. Abrasion of the former prevents comparison of the head, trochanter, and both condyles. The Pureni femur is longer, is more gracile, and has a straighter medial edge than those of *Emuarius gidju*. The sides of the shaft of *C. lydekkeri* are straighter, nearly parallel anteriorly, and less curved laterally. The curvature of the shaft where it joins the distal margin of the head is less in *C. lydekkeri* than in the Kutjamarpu specimen, causing its appearance to be more abrupt in the former. The popliteal area is longer in *C. lydekkeri*, extending farther toward the external condyle. On the anterior side, the external condyle of the Kutjamarpu femur appears, despite the abrasion, to curve more toward the long axis midline, the edge of the condyle and the rotular groove being about 30°–45° to midline, as compared to subparallel to 15° in *C. lydekkeri*. Using the heads of the femora as common reference points, the proximal-most point of the external condyle in anterior view is higher in the Kutjamarpu specimen than in the Pureni one, though damage prevents exact measurements. In anterior view, the medial edge of the internal condyle of the Kutjamarpu specimen is directed more anteriad and less parallel to the medial side of the shaft.

Tibiotarsus. Shaft anteroposteriorly compressed, rounded on posterior surface, flattened on anterior; sides straight, parallel. Tendinal groove apparent only on distal part of shaft, merging with general surface along medial edge, but bordered by ridge on lateral edge. Tendinal canal widening distad, ending in oval depression oriented proximolaterad-distomediad; along distal margin of depression is small ridge extending proximolaterad across anterior intercondylar fossa, then sharply proximad to lateral edge. Small foramen at or slightly distal to end of ridge, located proximal to fossa, and dorsal and lateral of shaft midline. External condyle oval to semicircular, rounded on anterodistal end, more flattened on posterodistal end. Joining of anterior surface of external condyle with shaft angular, not rounded;

Table 3. Measurements (mm) of tibiotarsi of *Emuarius gidju.*

	QM F16827	SAM P26779	AM 78586
Distal end			
1. Width across condyles	—	33.8±	—
2. Depth, internal condyle	—	>29.0	—
3. Depth, external condyle	33.7	31.0±	—
4. Width of distal end across internal ligamental prominence	—	33.6±	35.3±
5. Length, external condyle			
Anterior end	24.1	21.0	—
Posterior end	21.8	18.1	—
6. Length, internal condyle, anterior end	17.5	—	—
7. Length, anterior intercondylar fossa, midpoint	11.0±	8.6	—

joining of posterior surface rounded. Joining of anterior surface of internal condyle at about right angle. Anteriorly, external condyle longer than internal condyle; external condyle with greater proximal extension than internal condyle on both anterior and posterior surfaces; distal extension of condyles subequal.

As in *Casuarius,* the external condyle of *Emuarius* is distally rounded, rather than flattened, with the anterior half of its distal border curving more sharply proximad than in *Dromaius.* A small ridge is present at the distolateral end of the tendinal canal in *Casuarius, Dromaius,* and *Emuarius;* however, in *Dromaius* and *Emuarius,* it continues proximolaterad past the midline of the shaft; in *Casuarius* there is a muscle scar in this position, but it is not raised. The anterior surface of the shaft is flattened in *Emuarius* and *Dromaius* and slightly rounded in *Casuarius.* The distal end of the tibiotarsus is wider and deeper in *Emuarius* than in the dwarf emus.

The distal ends of tibiotarsi from Riversleigh sites are the only elements that are directly comparable to any part of the holotypic left leg; these exhibit several minor differences (Table 3). The proximal shaft of the holotypic element appears wider and deeper than Riversleigh QM F16827, but this is certainly at least a partial result of crushing and subsequent repair. However, Riversleigh AM F78586 is also wider and deeper. Its external condyle extends, in lateral view, farther anteriad and posteriad, and the angles between the shaft and the condyle are more abrupt. The distal edge of the condyle is perhaps less rounded, though abrasion prevents positive determination. In anterior view, the external condyle and the anterior intercondylar fossa are longer. The small ridge extending proximad from the anterior intercondylar fossa to the lateral edge is interrupted in AM F78586 by a gap. The distal edge of the anterior intercondylar fossa between the condyles varies from more or less flattened (AM F78586) to angularly concave (QM F16827). Possible differences in the holotype of the configuration and relative size of these and other features proximal to the anterior intercondylar fossa cannot be assessed. Also see Patterson and Rich (1987).

Tarsometatarsus. Considerably anteroposteriorly compressed, overemphasized in proximal shaft by substantial amount of crushing that prevents detailed assessment of surface features and proportions. Edges of shaft in anterior view straight, converging slightly distad. Medial border of internal cotyla flattened; lateral border of external cotyla noticeably convex laterally;

Table 4. Measurements (mm) of tarsometatarsi of *Emuarius gidju.*

	AM F78587	SAM P26779
Proximal end		
1. Width	—	36.8
2. Depth of internal cotyla	—	19.1
3. Depth of external cotyla	—	>16.8
4. Depth across intercotylar area to posterior extension of hypotarsus	—	27.2
Distal end		
5. Width	44.1	—
6. Width of trochlea II, anterior	>9.5	—
7. Width of trochlea III, anterior	19.1	—
8. Maximum width of trochlea IV, anterior	14.5	—
9. Depth of trochlea II		
Internal	>10.5	—
External	12.1±	—
10. Depth of trochlea III		
Internal	>19.8	—
External	20.0	—
11. Depth of trochlea IV, internal	13.4	—

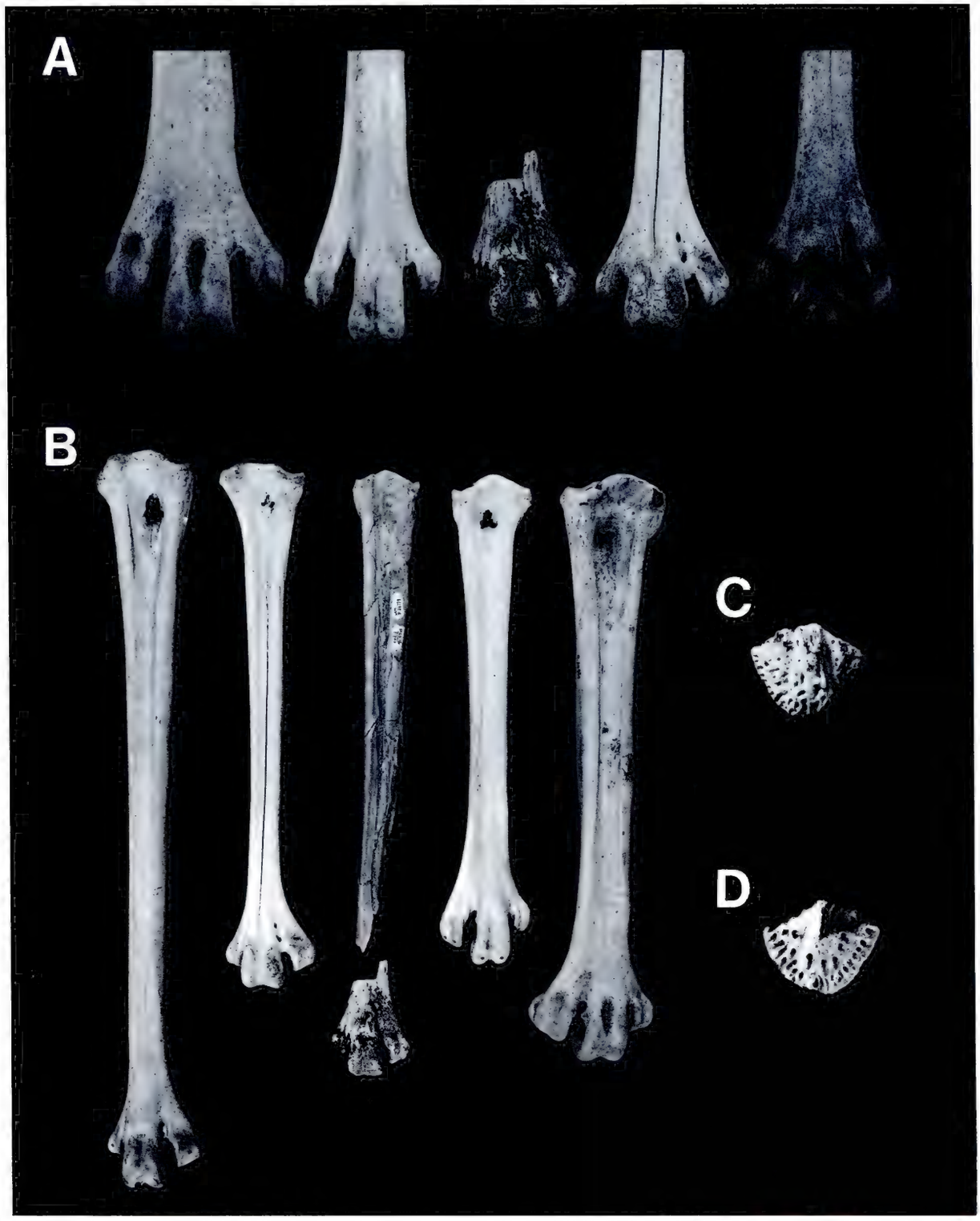

Figure 6. **A.** Left and right tarsometatarsi of casuariids, distal end, anterior view, 0.5×. Left to right: *Casuarius casuarius* (QM O20698), *C. bennetti* (AM O42539), *Emuarius gidju* (AM F78587), *Dromaius novaehollandiae* (AM S1515), *D. ater* (AM F15602). **B.** Tarsometatarsi of casuariids. Comparative lengths, that of *E. gidju* reconstructed using combined proximal (SAM P26779) and distal fragments (AM F78587). Left to right: *D. novaehollandiae* (AM S1515), *D. ater* (AM F15602), *E. gidju, C. bennetti* (AM O42539), *C. casuarius* (QM O20698), 0.33×. **C, D.** Maxilla of *E. gidju,* QM F16830, Upper Site local fauna, 2×, in (C) dorsal and (D) ventral views.

intercotylar region not extending as far proximad to articular surface as in *Casuarius;* width and depth of proximal articular surface less than in *Dromaius.* Hypotarsus appears less blocky or prominent than in *Casuarius.* External ligamental prominence above external ligamental pit less defined than in *Dromaius;* anterior ligamental fossa proportionally larger and deeper. Posterior metatarsal groove appears narrower with edges more angular, less rounded than in *Casuarius* or *Dromaius;* anterior metatarsal groove appears prominent proportionally farther distally along shaft. Trochleae II and IV not as splayed as in living *Casuarius,* more so than in *Dromaius;* trochleae II and IV more reduced than in *Casuarius,* less than in *Dromaius;* both trochleae extend farther posteriad, making plantar surface concave, though less so than in *Casuarius.* Shaft proximal to base of trochlea IV wider laterally than in *Dromaius.* Width and depth of trochleae subequal.

In *Casuarius, Dromaius,* and *Emuarius,* in anterior view, there is a groove along the shaft extending proximad from between trochleae III and IV. In *Dromaius,* at the proximal end of the groove, a foramen exists that extends anteroposteriad completely through the shaft, and at the distal end of the groove it is often roofed over slightly proximal to the bases of the trochleae. In *Casuarius* and *Dromaius,* the proximal foramen is absent and the distal foramen extends anteroposteriad completely through the shaft.

There is no distal tarsometatarsus preserved in the holotype, but in size the Riversleigh specimen matches the included proximal portion. Also see Patterson and Rich (1987).

Pes. Overall, phalanges more dorsoventrally compressed than in *Casuarius* but less so than in *Dromaius,* though often approaching the latter; laterally compressed, more gracile than in living emus and cassowaries. Intercondylar fossa deep; plantar divergence of condyles moderate. On proximal end, medial prominence proportionally longer and lateral prominence proportionally shorter than in living forms. Lengths of digits II and IV relative to digit III greater than in *Dromaius.* Ungual phalanx of digit II not developed into spike; ungual III weakly developed. Also see Patterson and Rich (1987).

DISCUSSION

WHY ONE, NOT TWO, SPECIES?

Although Patterson and Rich (1987) interpreted the holotypic hindlimb of *Emuarius gidju* to be that of an emu, the Kutjamarpu femur by itself would be placed in *Casuarius.* The occurrence of both the cassowary-like femur and the emu-like lower limb in the various Riversleigh deposits and in the Kutjamarpu local fauna can be interpreted in two ways: either two small ratites of similar size, one an emu and one a cassowary, existed contemporaneously at both locations; or there is one small ratite at both sites that exhibits a combination of emu and cassowary features. For reasons discussed later, the second interpretation is accepted here.

The apparent affinities of the various hindlimb elements, initially evident in the Kutjamarpu material, have been confirmed by additional finds. Had two sympatric forms existed, this consistent division in skeletal elements would be unexpected; emu-like femora and cassowary-like tibiotarsi should have been found.

It seems unlikely that two closely related, flightless, terrestrial species of such similar size would occur together, although there are few examples among modern ratites with which to make a comparison. In New Guinea, the distribution of the dwarf *Casuarius bennetti* considerably overlaps that of the large *C. casuarius,* and it has a smaller overlap with the range of the other large species, *C. unappendiculatus* (Mayr, 1979). The two large cassowaries have only slight contact through most of New Guinea, making only marginal contact in the central ranges, but they do meet through most of the Vogelkop (Fig. 1). Although no work has been carried out to demonstrate the actual extent of sympatry or possible interactions, this may be the only significant instance of two similar-sized species of the Casuariidae (*sensu lato*) occurring together. Elsewhere a considerable size difference is found between sympatric species.

A small fossil emu, the size of the insular pygmy *Dromaius ater,* has been found on the Australian mainland (Patterson and Rich, 1987). Its relationship to the dwarf emus is not known; neither are its affinities to *D. novaehollandiae* understood at present. If this form is not an instance of dwarfism in *D. novaehollandiae,* and if it does represent a distinct species, then its occurrence would present an analogous example of sympatry comparable to that of the cassowaries.

The larger, superficially similar dromornithids, which were also sympatric with *Emuarius gidju,* may have also exerted restraints on casuariid body size through resource partitioning by occupying the upper end of the size spectrum of flightless terrestrial birds. The two dromornithid taxa represented at Riversleigh are *Barawertornis tedfordi* Rich 1979 (about the size of a modern *Casuarius casuarius*) and a much larger form, cf. *Bullockornis planei* Rich 1979 (about twice the size of *Barawertornis tedfordi*).

Mammalian taxa from the Riversleigh local faunas show correlations with elements of the Kutjamarpu local fauna (see Geographic and Geological Setting). The Riversleigh and Leaf Locality paleocommunities are interpreted to have been densely vegetated, probably with rain forest (Archer et al., 1988, 1989). Such a habitat would not favor emus as they are understood today: In Australia, emus and cassowaries show strong differences in habitat preferences, with emus occupying drier, more open habitats. The preferences of modern taxa, however, are questionably relevant to ancestral forms and, indeed, Patterson and Rich (1987) considered that *Dromaius* (=*Emuarius*) *gidju* would have differed from modern emus by having a less cursorial life-style. This would further reduce the ecological differences between a small emu and a small cassowary existing sympatrically. For these reasons, it is doubtful that the postulated habitat of the Leaf Locality could have supported a small emu and a small cassowary with requirements similar to those of the extant forms. If the requirements were less restricted than for modern forms, this should have led to greater overlap in habitat use. Such would not be expected for two similarly sized and closely related forms.

Although I consider only a single taxon to be represented by the material discussed herein, there are differences between the Kutjamarpu and Riversleigh specimens. The limited fossil material precludes any assessment of whether sex, age, or individual variation is involved, and these have yet to be evaluated in a systematic manner for any living taxon. An additional consideration is that the differences may reflect real population variation but that the specimens represent different "chronospecies" from different time stages in the evolution of a single lineage. The ages of the various deposits are far from confirmed, but they may have a temporal range from Late Oligocene to Middle Miocene (25–15 Ma). The extremes of this range yield differences of 10 million years between Kutjamarpu and Riversleigh or even between the various Oligocene/Miocene Riversleigh local faunas. If this were the case, the observed variation in the limb bones could be attributable to anagenetic change over this period, rather than as indicative of a cladogenetic event. Ad-

Table 5. Measurements (mm) of pedal phalanges of *Emuarius gidju*.

	SAM 26779 (left leg)				
Phalanx:	1	2	3	1	2
Digit:	II	II	II	III	III
1. Total length	33.0	23.7	19.1	45.2	31.8
2. Maximum width, proximal end	13.0	11.9	9.0	19.4	15.1
3. Maximum width, distal end	11.2	9.3	—	15.6	12.5
4. Maximum depth, proximal end	14.2	12.0	10.5	16.8	13.0
5. Depth, internal condyle	10.5	7.6	—	12.3	9.3
6. Depth, external condyle	12.7	9.1	—	12.2	9.0

	Digit II	Digit III	Digit IV
Total length			
With ungual phalanx	75.8	117.6	80.8
Without ungual phalanx	56.7	99.4	65.2

ditional material and more accurate dating of deposits are needed to clarify these points.

HINDLIMB MORPHOLOGY AND LOCOMOTORY MODE

In its structure, the foot of *Emuarius gidju* is more like that of emus than that of cassowaries. It is, however, more cassowary-like than any known species of *Dromaius*. Its phalanges are substantially more dorsoventrally compressed than those of *Casuarius*, being similar to, though less compressed than, the condition in *Dromaius*. The ungual phalanx of digit II, while not developed into a spike as in *Casuarius*, is longer than that of digit III (Tables 1, 5; Fig. 2); in emus, the ungual phalanx of digit III is longer. Digit II of *Emuarius* is comparatively longer than in emus, as is digit IV, though not to the same degree (ratios of II:III and IV:III, respectively, without ungual phalanges: *Casuarius*, 0.82, 0.76; *Emuarius*, 0.57, 0.68; *Dromaius*, 0.55, 0.63). Patterson and Rich (1987) suggested that the reduction of digit IV and particularly of digit II in *E. gidju*, compared with the highly cursorial *D. novaehollandiae*, appears to parallel similar reductions in other groups of terrestrial birds and mammals. This foot structure presumably permitted greater maneuverability in habitat less open than that used by emus today.

Another feature by which *Emuarius gidju* more closely resembles *Casuarius* than *Dromaius novaehollandiae* is the high, arched intercotylar prominence of the tarsometatarsus. However, the extinct *D. ocypus* also exhibits this condition, the functional significance of which is unclear.

One of the characters cited by Patterson and Rich (1987) and Rich et al. (1988) for separating cassowaries and emus is the relative proximal extent of the external and internal condyles of the femur in anterior view: In *Casuarius*, these are subequal; in *Dromaius*, the external condyle extends decidedly farther. This character may correlate more strongly with the extent of cursoriality than with the degree of relationship. The cursorial Ostrich, *Struthio camelus*, and rheas (*Rhea americana* Linnaeus 1758, *Pterocnemia pennata* Orbigny 1834) have external condyles with decidedly greater proximal extents than the internal condyles. The flightless dromornithids ranged in form from graviportal to cursorial (Rich, 1979). The femora of graviportal taxa, such as *Dromornis stirtoni* Rich 1979 and *Bullockornis planei* Rich 1979, have condyles more nearly equal in proximal extent than does the more cursorial *Ilbandornis woodburnei*, in which the external condyle has the greater proximal extent. This suggests that the relative proximal extent of the condyles may be related to the mode of locomotion, and thus among the casuariids this feature merely reflects relative degrees of cursoriality. *Emuarius gidju* has the relative proximal extents of the condyles intermediate between the conditions in species of *Casuarius* and *Dromaius*.

PALEOENVIRONMENT AND CURSORIALITY

Species of *Casuarius* have long been considered the more primitive of the extant casuariids on the basis of both morphology and distribution (Rich and van Tets, 1982). Their graviportal locomotion is associated with moving through the dense vegetation of the Australo-Papuan rain forests. Throughout most of the Tertiary, much of Australia was covered in closed forest, and the climate was considerably more humid than at present (Frakes et al., 1987). Temperate rain forest was considered to have been the dominant vegetation type over much of the continent and certainly along watercourses. Drying of the climate and appearance of open habitats on a large scale did not take place until at least the Middle Miocene, ca. 15 Ma, if not later. Increased cursoriality seems related to the appearance of more open habitat. *Emuarius gidju* appears to mark in the Casuariidae a stage in the transition to more cursorial locomotion, which suggests that at least some replacement of closed forest by more open habitat was taking place by the Early Miocene. The possibility that the ground cover of the rain forests was sufficiently open for cursorial animals cannot be unequivocably ruled out. Palynological analysis has indicated the presence of *Nothofa-*

Table 6. Measurements (mm) of the scapulocoracoid of *Emuarius gidju*.

	QM F16831
1. Minimum mediolateral width, coracoid shaft	9.8
2. Length, glenoid facet	10.5
3. Depth, glenoid facet dorsoventral of midpoint	10.0
4. Maximum depth in glenoid area	12.0

Table 5. Continued.

3	4	1	2	3	4	5
III	III	IV	IV	IV	IV	IV
22.4	18.2	29.3	16.2	10.9	8.8	15.6
13.0	10.5	14.2	11.0	9.6	8.2	8.0
10.1	—	11.1	9.3	8.6	7.9	—
10.6	10.1	12.8	11.4	9.2	7.9	8.9
7.8	—	11.5	8.6	8.9	7.8	—
7.0	—	9.0	7.4	6.8	6.2	—

gus-dominated rain forest in the Lachlan River district of New South Wales during the Late Eocene through the Late Oligocene–Early Miocene (Martin, 1987). Modern *Nothofagus* forests frequently open below the canopy, without the dense understory of some other rain forest types (pers. obs.).

Originally thought to be Middle Miocene (15 Ma), some of the Riversleigh deposits containing the *Emuarius gidju* material are now considered to be closer to Lower Miocene or even Upper Oligocene (25 Ma) (Archer et al., 1989). The presence of *E. gidju* in these faunas implies that the separation of cassowaries and emus had already taken place by this time. Sibley and Ahlquist (1991), using DNA-DNA hybridization, timed the cassowary–emu division at 20–25 Ma. The degree of cursoriality in *E. gidju* suggested by the hindlimb characters suggests that this form postdated the cladistic event and, although probably close to the mutual ancestor of emus and cassowaries, could not itself have been that ancestor. If only two subfamilies are maintained within the Casuariidae, as is done here, then *Emuarius* should be included in the Dromaiinae.

SUMMARY AND CONCLUSION

Emuarius gidju probably looked much like a small, gracile emu, about the size of an Australian Bustard *Ardeotis australis*. Presumably its mode of locomotion was somewhat intermediate between emus and cassowaries, but this requires further investigation. New tibiotarsal and tarsometatarsal material will permit determination of the absolute lengths and relative proportions of the hindlimbs. Because the lengths of the neck and legs are generally roughly equivalent in long-legged birds such as emus and cassowaries, the hindlimb lengths will allow an estimate of the overall size of *E. gidju*. Hindlimb proportions will provide

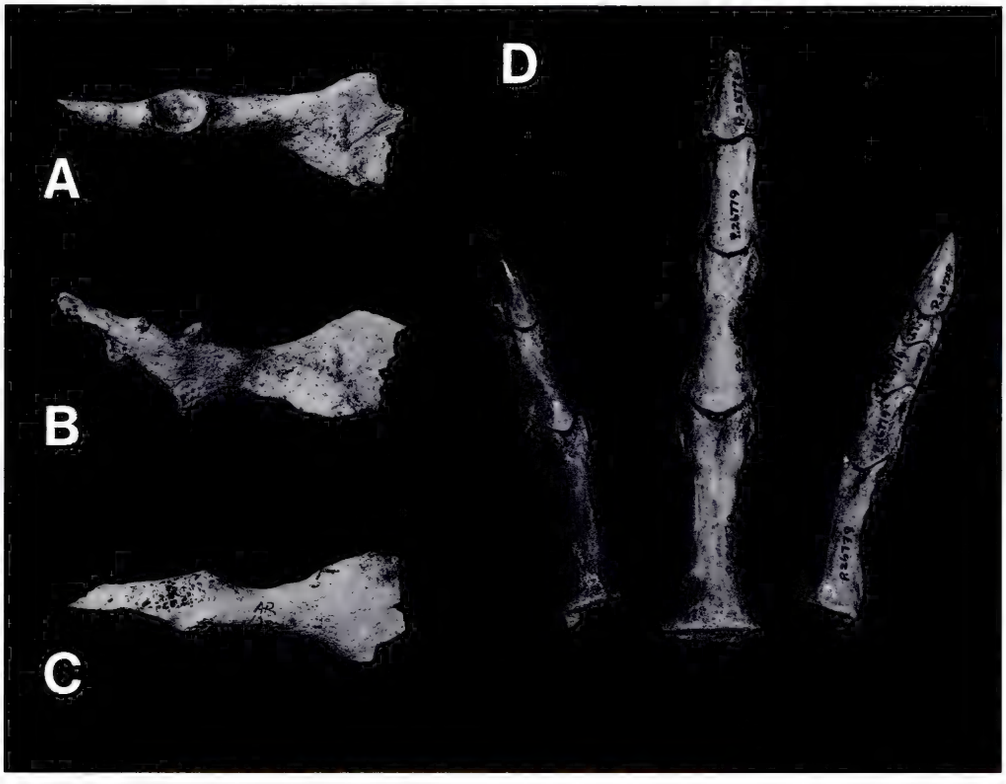

Figure 7. Bones of casuariids. **A–C.** Right scapulocoracoid of *Emuarius gidju,* QM F16831, Upper Site local fauna, 1×, in (**A**) lateral, (**B**) dorsal, and (C) ventral views. **D.** Left pedal phalanges of *E. gidju,* SAM P26779 (holotype), Kutjamarpu local fauna, 1×.

an indication of its degree of cursoriality and allow comparisons with Recent forms. These will grant greater insight into the evolution of the Australian ratites and their adaptation to the Tertiary opening of the Australian landscape.

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NEW DATA CONCERNING *PALAELODUS AMBIGUUS* (AVES: PHOENICOPTERIFORMES: PALAELODIDAE): ECOLOGICAL AND EVOLUTIONARY INTERPRETATIONS

Jacques Cheneval and
François Escuillié

ABSTRACT. The discovery of an almost complete skeleton, with an associated fragmentary skull, attributable to the flamingo-like fossil bird *Palaelodus ambiguus,* permits the first description of palaelodid skulls. The important characters of the skull are (1) presence of two deep grooves separated by a ridge on the interorbital part of the frontal, which may indicate the presence of salt glands; (2) foramen magnum large; (3) presence of two large occipital fontanelles above the foramen magnum; (4) basitemporal plate flat and sphenoidal rostrum thick; (5) temporal fossa comparatively larger and deeper than those in flamingos; (6) opisthotic fossa low and not expanded; and (7) maxillary straight, short, and fairly large. The description of the *Palaelodus* skull and of the sparse remains of lower jaws, and a comparison of these with filter-feeding species, suggest that palaelodids may have developed a primitive filter-feeding apparatus. The characters of the skull emphasize the affinities of the palaelodids with modern flamingos.

The new data on the palaelodid skull enable the referral of the skull material of the fossil crane species *Probalearica problematica* and of the *incertae sedis* species *Ibidopodia palustris* to *Palaelodus ambiguus.* This points out the need for a new study of the remaining material of *Probalearica.*

RÉSUMÉ. Un squelette d'oiseau presque complet a été récemment découvert dans une des grandes carrières de la région de Saint-Gérand-le-Puy (Allier, France). Ce squelette, accompagné d'un crâne très fragmentaire, est atrribué à l'espèce fossile *Palaelodus ambiguus,* proche des flamants actuels. Le crâne associé permet la première description sûre du crâne des Palaelodidae.

Les principaux caractères distinctifs du crâne des Palaelodidae sont les suivants: (1) présence de deux gouttières profondes, séparées par une petite crête, sur la partie interorbitaire du frontal (ces gouttières indiqueraient la présence de glandes à sel); (2) foramen magnum large; (3) présence de deux larges fontanelles occipitales juste au dessus du foramen magnum; (4) plancher basitemporal très plat et rostre sphénoidal épais; (5) fosses temporales très larges et assez profondes; (6) fosses opisthotiques peu étendues et basses; (7) bec très droit, assez court et relativement large. Ces caractères soulignent notamment les affinités des Palaelodidae avec les flamants actuels.

La détermination du crâne de *Palaelodus* et la description des restes très abîmés de mandibule inférieure permettent, par comparaison avec ce que l'on observe chez différents oiseaux filtreurs, de suggérer que les Palaelodidae avaient probablement développé un appareil filtreur, certes bien plus primitif que celui des véritables flamants qui sont en ce domaine les oiseaux les plus perfectionnés.

Ces nouvelles données permettent de mettre en synonymie avec *Palaelodus ambiguus* le matériel crânien précédemment décrit comme appartenant à une grue fossile, *Probalearica problematica,* ou à un oiseau énigmatique, *Ibidopodia palustris* (placé pour le moment en *incertae sedis*). Ceci pose un problème, tout particulièrement pour le genre *Probalearica* dont le matériel crânien représentait le lectotype; une nouvelle étude des grues fossiles de Saint-Gérand-le-Puy permettra certainement de résoudre cette question.

Key words: *Palaelodus,* ecology, flamingos, Tertiary birds, evolution.

INTRODUCTION

Gervais (1848–1852) was the first author to describe, but not name, palaelodid fossils from Miocene deposits of the Saint-Gérand-le-Puy area of France, at which time he compared this material with other wading birds such as the avocet, the curlews, the moorhen, and the plovers.

Subsequently, Milne-Edwards (1863) established the genus *Palaelodus* for this material and described three species: *P. ambiguus, P. crassipes,* and *P. gracilipes.* At a later date, he described two other species: *P. minutus* and *P. goliath* (Milne-Edwards, 1867–1871). Other authors (Lydekker, 1891; Lambrecht, 1933; Brodkorb, 1963a) came to the same determinations.

In a review of the French material, Cheneval (1983a, 1983b) recognized three species of *Palaelodus: P. ambiguus, P. gracilipes,* and *P. crassipes.* He placed *P. minutus* into synonymy with *P. gracilipes* and transfered *P. goliath* to the genus *Megapaloelodus* Miller 1944 (Cheneval, 1983a). Material referred to *Megapaloelodus* had previously been known only from the Miocene of South Dakota (Miller, 1944).

Palaelodid material is particularly abundant at Saint-Gérand-le-Puy, and all species are very well known. The total number of specimens studied for each *Palaelodus* species is: for *P. ambiguus,* 8,333 bones, at least 477 minimum number of individuals (MNI); for *P. gracilipes,* 690 bones, 55 MNI; for *P. crassipes,* 320 bones, 32 MNI; and for *Megapaloelodus goliath,* 63 bones, 13 MNI. The osteological study of these birds (Cheneval, 1983a, 1983b) suggested that they are closely related to the family Phoenicopteridae, with possible affinities with the families Anatidae and Recurvirostridae.

However, an exasperating problem has been the absence of skulls in this abundant material. Milne-Edwards (1867–1871:pl. 82; pl. 84, figs. 9–11) attributed a fragment of bill to *Palaelodus*

ambiguus, while another very similar bill was attributed to the fossil crane *Probalearica problematica* (Milne-Edwards, 1867–1871:pl. 76, figs. 5–7). These two bills are also very similar to that attributed by Milne-Edwards (1867–1871:pl. 71, figs. 13–16) to the species *Ibidopodia palustris* Milne-Edwards 1867–1871, currently considered *incertae sedis*. More recently, Cracraft (1973) assigned all this material to *Probalearica problematica*, but Olson and Feduccia (1980b) were skeptical about this identification. Rothausen (1966) also attributed a skull from Miocene deposits in Germany to *Palaelodus*. As mentioned earlier, all of these skulls and bills are considered by us to be similar, but there was no certitude about whether this material belonged to *Palaelodus* or *Probalearica* Lambrecht 1933.

During an outing to the quarry "Les Pérards," near the village of Montaigu-le-Blin, Saint-Gérand-le-Puy area, in November 1985, one of us (F.E.) discovered an almost complete articulated skeleton of a medium-sized bird. This skeleton is referred to the fossil species *Palaelodus ambiguus*. The frontal portion of a fragmentary skull was discovered at a distance of about 1 m from this skeleton; because no other fossil remains were in the vicinity, there is little doubt that this skull belonged to the same individual as the articulated skeleton. This skull fragment is very similar to the frontal part of the skulls previously described as *Palaelodus*, *Probalearica problematica*, and *Ibidopodia palustris*. Apparently all of these skulls can now be referred to *Palaelodus*. We present here a description of this material and an interpretation of the life habits of these strange, flamingo-like birds.

GEOLOGICAL SETTING

The Agenian terrains of the Saint-Gérand-le-Puy area are situated in the "Limagne bourbonnaise" sedimentary basin in the center of the Massif Central near the Allier River. The history of the Limagne Basin is connected with the formation of the Alps mountain range. The down-warping of this basin began in the Eocene; during the Late Oligocene (Chattian) and the Early Miocene (Agenian), the area was covered with lacustrine depressions that were more or less independent of each other. From these expanses of water originated limestone deposits whose appearance and structure are now very different. Subsequently, the lakes dried out, and the Limagne Basin has now been under the influence of river erosion for some time.

The quarries of the Saint-Gérand-le-Puy area were first exploited for the production of lime, which continued for more than a century and a half, and more recently for the production of cement. Most quarries were filled in at the end of quarrying, but "Les Pérards" is still an active quarry. In this quarry, open since the end of the last century, reef limestone that originated as algal spreads (stromatolitic "choux-fleurs") provides an abundant invertebrate and vertebrate fossil fauna. The reef limestone can be more than 20 m thick (Bucher et al., 1985).

Vertebrate remains are usually found in non-limestone deposits, coming from green marls with "*Cypris*" (ostracods), and bioclastic sands of the northwest working face of the quarry. The green marls fauna comprises species of aquatic habits (e.g., *Palaelodus* in abundance and anatids). Beaver specimens of the species *Steneofiber eseri* von Meyer 1846 (family Castoridae) are also present.

The associated palaelodid skeleton was discovered in one of the green marl horizons, halfway up an old southeast working face. It was situated in the upper limit of a clayey layer. Bones of the skeleton were either trapped in the mass of clayey layer or, to a larger degree, protruding into the interface with the sand layer above. Some of the cervical vertebrae seem to have been lost during the deposition of the sand layer. The pectoral girdle and the sternum appear to have been destroyed during exploitation of the working face. In other places within the quarry, a few remains of juvenile *Palaelodus* were found in the same clayey layers of the same green marl horizon.

The skeleton was oriented in an east–west direction. The orientation of the neck and jaws indicates that the local water stream was coming from the East, but a general direction for water flow cannot be determined by one specimen.

METHODS AND MATERIALS

Skull and bone measurements are after those from Driesch (1976). The osteological nomenclature is from Howard (1929, 1980).

The fossil skull specimens were compared especially with the skulls of the following modern birds.

- Diomedeidae: *Diomedea exulans* (Wandering Albatross), *D. nigripes* (Black-footed Albatross), *Phoebetria palpebrata* (Light-mantled Sooty Albatross)
- Procellariidae: *Macronectes giganteus* (Southern Giant Petrel), *Fulmarus glacialis* (Northern Fulmar), *Daption capense* (Cape Pigeon), *Pachyptila vittata* (Broad-billed Prion), *Procellaria cinerea* (Grey Petrel), *Puffinus carneipes* (Flesh-footed Shearwater), *P. griseus* (Sooty Shearwater)
- Hydrobatidae: *Pelagodroma marina* (White-faced Storm-Petrel), *Hydrobates pelagicus* (Storm-Petrel), *Oceanodroma leucorhoa* (Leach's Storm-Petrel)
- Spheniscidae: *Pygoscelis papua* (Gentoo Penguin), *P. antarctica* (Ringed Penguin), *Eudyptes chrysocome* (Rockhopper Penguin), *E. pachyrhynchus* (Fiordland Crested Penguin)
- Gaviidae: *Gavia stellata* (Red-throated Loon), *G. immer* (Common Loon)
- Threskiornithidae: *Eudocimus albus* (White Ibis), *Plegadis falcinellus* (Glossy Ibis), *Bostrychia hagedash* (Hadada Ibis), *Threskiornis aethiopicus* (Sacred Ibis), *Pseudibis papillosa* (White-shouldered Ibis)
- Phoenicopteridae: *Phoenicopterus ruber* (Greater Flamingo), *Phoenicoparrus andinus* (Andean Flamingo)
- Anatidae: *Dendrocygna bicolor* (Fulvous Treeduck), *D. viduata* (White-faced Treeduck), *Cygnus olor* (Mute Swan), *C. columbianus* (Whistling Swan), *Anser albifrons* (Greater White-fronted Goose), *A. anser* (Grey-lag Goose), *Branta canadensis* (Canada Goose), *B. bernicla* (Brant), *Alopochen aegyptiaca* (Egyptian Goose), *Tadorna tadorna* (Common Shelduck), *Plectropterus gambensis* (Spur-winged Goose), *Sarkidiornis melanotos* (Knob-billed Goose), *Nettapus auritus* (Pygmy Goose), *Aix sponsa* (Wood Duck), *Anas strepera* (Gadwall), *A. crecca* (Green-winged Teal), *A. platyrhynchos* (Mallard), *A. acuta* (Pintail), *A. querquedula* (Garganey), *Netta rufina* (Red-crested Pochard), *Aythya ferina* (Common Pochard), *A. fuligula* (Tufted Duck), *A. marila* (Greater Scaup), *Somateria mollissima* (Common Eider), *Clangula hyemalis* (Oldsquaw), *Melanitta nigra* (Black Scoter), *M. fusca* (Velvet Scoter), *Bucephala clangula* (Common Goldeneye), *B. albeola* (Bufflehead), *Mergus cucullatus* (Hooded Merganser), *M. serrator* (Red-breasted Merganser)
- Gruidae: *Grus grus* (Common Crane), *G. antigone* (Sarus Crane), *Anthropoides virgo* (Demoiselle Crane), *Balearica pavonina* (Crowned Crane)
- Rostratulidae: *Rostratula benghalensis* (Painted Snipe)
- Haematopodidae: *Haematopus ostralegus* (Common Oystercatcher)

- Recurvirostridae: *Recurvirostra avosetta* (Common Avocet)
- Charadriidae: *Vanellus vanellus* (Common Lapwing), *V. spinosus* (Spur-winged Plover), *V. indicus* (Red-wattled Lapwing), *Pluvialis apricaria* (Greater Golden Plover), *P. dominica* (Lesser Golden Plover), *P. squatarola* (Grey Plover), *Charadrius hiaticula* (Ringed Plover), *C. vociferus* (Killdeer)
- Scolopacidae: *Scolopax rusticola* (Eurasian Woodcock), *S. minor* (American Woodcock)
- Stercorariidae: *Stercorarius skua* (Great Skua), *S. pomarinus* (Pomarine Jaeger), *S. parasiticus* (Parasitic Jaeger), *S. longicaudus* (Long-tailed Jaeger)
- Laridae: *Larus argentatus* (Herring Gull), *L. fuscus* (Lesser Black-backed Gull), *L. marinus* (Great Black-backed Gull), *L. glaucescens* (Glaucous-winged Gull), *L. ridibundus* (Black-headed Gull), *L. tridactylus* (Black-legged Kittiwake), *L. sabini* (Sabine's Gull), *Sterna nilotica* (Gull-billed Tern), *S. hirundo* (Common Tern), *S. albifrons* (Little Tern), *S. sandvicensis* (Sandwich Tern)
- Alcidae: *Plautus alle* (Dovekie), *Alca torda* (Razorbill), *Uria lomvia* (Thick-billed Murre), *U. aalge* (Common Murre), *Cepphus grylle* (Black Guillemot), *C. columba* (Pigeon Guillemot), *Synthliboramphus antiquus* (Ancient Murrelet), *Ptychorhamphus aleuticus* (Cassin's Auklet), *Aethia pusilla* (Least Auklet), *A. pygmaea* (Whiskered Auklet), *Cerorhinca monocerata* (Rhinoceros Auklet), *Fratercula arctica* (Common Puffin)

All of the skulls of modern birds are from the collections of the Centre des Sciences de la Terre, Université Claude Bernard–Lyon I.

Abbreviations used in the text are as follows: FSL, Centre des Sciences de la Terre, Université Claude Bernard–Lyon I, Villeurbanne; ML, Musée Guimet d'Histoire naturelle, Lyon; and MNHN, Muséum national d'Histoire naturelle, Institut de Paléontologie, Paris.

SYSTEMATICS

Order Phoenicopteriformes Sharpe 1891

Family Palaelodidae (Stejneger 1885)

Palaelodontidae Stejneger, 1885:154.
Palaelodidae Fürbringer, 1888:1565.
Paloelodidae Howard, 1955:22.

Genus *Palaelodus* Milne-Edwards 1863

Palaelodus Milne-Edwards, 1863:158 (original description); Cheneval, 1983a:180.
Pars *Ibidopodia* Milne-Edwards, 1867–1871:Vol. 1, 465 (original description).
Paloelodus Milne-Edwards, 1867–1871:Vol. 2, 58; Rothausen, 1966:26.
Pars *Probalearica* Lambrecht, 1933:519 (original description); Cracraft, 1973:87.

TYPE SPECIES. *Palaelodus ambiguus* Milne-Edwards 1863.

INCLUDED SPECIES. Type species; *P. crassipes* Milne-Edwards 1863; *P. gracilipes* Milne-Edwards 1863; *P. steinheimensis* Fraas 1870 [Olson and Feduccia (1980b) consider this species to be a large anseriform].

DIAGNOSIS. See Cheneval (1983a:181).

REMARKS. In the first studies of the genus, two orthographies were employed: *Palaelodus* and *Paloelodus*. In the books of Milne-Edwards (1863, 1867–1871), the italic writing of the two diphthongs *-ae-* and *-oe-* is the same, but the Roman writing and the Greek etymology demonstrate that only the spelling *Palaelodus* is correct.

Table 1. Measurements (mm) of *Palaelodus ambiguus* skulls. Abbreviations: GL, greatest length; CBL, condylobasal length; GBP, greatest breadth across the postorbital process; SBO, smallest breadth between the orbits; GH, greatest height in the median plane; LP, length from the occipital protuberance to the most aboral points of the frontal process; LI, length of the upper jaw (=incisivum) (measurements after Driesch, 1976).

	FSL 444220	MNHN Av 8730	ML S'G 60
GL	—	89.90	83.74±
CBL	—	—	78.50
GBP	—	—	27.10
SBO	8.00±	7.00±	7.70
GH	—	—	24.68
LP	—	44.28	40.00
LI	—	46.00±	44.00

Palaelodus ambiguus Milne-Edwards 1863

Figures 1–9

Palaelodus ambiguus Milne-Edwards, 1863:159 (original description); Cheneval, 1983a:181, pl. 1, fig. 1.
Pars *Ibidopodia palustris* Milne-Edwards, 1867–1871:Vol. 1, 465, pl. 71, figs. 13–16; Cheneval, 1983b:120.
Pars *Grus problematica* Milne-Edwards, 1867–1871:Vol. 2, 30, pl. 76, figs. 5, 6 (original description).
Paloelodus ambiguus Milne-Edwards, 1867–1871:Vol. 2, 60, pls. 82–85; Rothausen, 1966:1, fig. 1.
Pars *Probalearica problematica* Lambrecht, 1933:519 (*nov. gen.*); Cracraft, 1973:88, fig. 40.

ORIGINAL MATERIAL. See Cheneval (1983a, 1983b).

REFERRED MATERIAL. Almost complete skeleton, FSL 444220; skulls, MNHN Av 8730 (figured in Milne-Edwards, 1867–1871:pl. 71, figs. 13–16, as *Ibidopodia palustris*), ML S'G 60 (labeled "*Hidopodia palustris*," *lapsus calami* for *Ibidopodia palustris*); fragmentary bill, MNHN Av 8728 (figured in Milne-Edwards, 1867–1871:pl. 76, figs. 5, 6, as *Grus problematica*).

HORIZON AND LOCALITY. Lower Miocene (Agenian) deposits; Saint-Gérand-le-Puy, Dept. Allier, France.

DIAGNOSIS. See Cheneval (1983a, 1983b).

MEASUREMENTS. For measurements of the skulls, see Table 1.

DESCRIPTION AND COMPARISONS. The almost complete skeleton (FSL 444220) lies on its back on the slab, the bones extending in a large circle. Most of the cervical vertebrae describe a large arc on the left edge of the slab (Fig. 1). There are four cervical vertebrae, with the first preserved vertebra close to the lower jaws, which are a little crushed one upon the other. A large space with only some traces of bone on the slab follows, where the vertebrae were not preserved, and then there are another five cervical vertebrae. The bones of the two wings occur near the last preserved vertebra; they are intermingled, with an acute, almost right angle between the ulnae and humeri. The bones of the left wing lie on top of those of the right wing (Figs. 1, 2). The left wing is better conserved than is the right,

rm
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ltm

with the carpometacarpus and phalanx 1 of digit II turned alongside the ulna. The ulna and radius of the right wing lie under the left humerus and carpometacarpus, and the right humerus is almost parallel with the left humerus. The distal part of the carpometacarpus lies under the last cervical vertebrae. All of the wing bones are badly fragmented. There are no remains of the pectoral girdle, nor of the sternum.

There are some fused thoracic vertebrae near the right humerus. The pelvis is exposed in ventral view, with the synsacrum and sacral vertebrae present. The two hindlimbs project from both sides of the pelvis (Figs. 1, 3). The two femora are fairly well preserved, but the head of the left one is somewhat crushed. The two tibiotarsi are crushed into a multitude of fragments. The two tarsometatarsi are very well preserved, and along with those of the left wing, they are almost the only well-preserved bones of the skeleton. The right tarsometatarsus rests across the proximal end of the left one as if the bird were sitting on a chair with the right leg crossed on the left one! There are no pedal phalanges.

This skeleton is undoubtedly a new individual of the species *Palaelodus ambiguus.* All of the sufficiently well-preserved bones show the characteristics of this species (for a description of *P. ambiguus,* see Cheneval, 1983a, 1983b). The few measurements that can be taken (i.e., greatest length for left tarsometatarsus, 114.2 mm; for right tarsometatarsus, 114.0 mm; for right carpometacarpus, 71.4 mm) are compatible with those for *P. ambiguus* (for complete measurements of *P. ambiguus,* see Cheneval, 1983a, 1983b).

The two mandibles are very crushed; therefore, no description of them is possible, but it can be seen that the mandibles had a great height.

No cranial material was found directly connected to the postcranial skeleton, but the frontal part of a braincase was found in the immediate vicinity of the skeleton (Fig. 4). As there were no other remains of fossil birds in the area where the skeleton was discovered, we can safely assume that this fragmentary skull came from the articulated skeleton. This fragment is very similar to the two skulls previously described as *Probalearica problematica* (Cracraft, 1973) and *Ibidopodia palustris* (Milne-Edwards, 1867–1871).

These cranial specimens (MNHN Av 8730 and ML S^{t}G 60) are preserved in fairly good condition. The skull referred to *Ibidopodia palustris,* MNHN Av 8730, has its ventral floor completely masked by matrix, its braincase is broken in places, and its bill is also partially covered by a thin layer of matrix (Fig. 5). The fragility of the remains precludes making any attempt to clean them. On the other hand, the skull referred to *Probalearica problematica,* ML S^{t}G 60, is in a better state of preservation, without matrix, but the broken bill has been reaffixed to the braincase with an ugly black mixture (Figs. 6–9).

These two partial skulls are very similar to one another, and also to the fragmentary braincase discovered in the vicinity of the articulated skeleton. This is especially true for the shape of the anterior part of the frontal, which bears, between the two orbits, two deep grooves divided by a slender and very prominent ridge. In some families of birds, these grooves indicate the presence of salt glands. However, the fossil remains differ from all of these families, especially in the forward position of the grooves (Fig. 7). In procellariiforms, the grooves extend more into the postorbital part of the frontals; in the other families (i.e., Pheniscidae, Gaviidae, Stercorariidae, Laridae, and Alcidae), they extend all along the orbits. The remains also differ from procellariiforms in the posteriorly convex parietal, which is very flattened and oblique in the shearwaters. They differ from skulls of the family Spheniscidae in having a very dorsally convex frontal, by lacking lateral ridges on the parietal, and by their comparatively small temporal fossa. The absence of lateral ridges and the small temporal fossa also separate the fossil remains from the Gaviidae. Members of the families Stercorariidae and Laridae have large postorbital processes, large temporal fossae, and flattened parietals. In the Alcidae, the frontal is much more flattened, and the temporal fossa is larger and extends more onto the dorsal area of the braincase than in the fossil skulls. So, among the birds with salt glands, the fossil remains are much more similar to the flamingos in their characters, i.e., the convex frontal, the prominent parietal, and the relative smallness of the temporal fossa. On the other hand, the presence of grooves on the frontal of the skull referred to *Probalearica* do not square with the description of a crane (Fig. 7), and we can assume that this skull is not referable to the family Gruidae.

Another important character seems to be the presence of two large occipital fontanelles above the foramen magnum on the posterior face of the braincase. These can be seen on the skull referred to *Probalearica* (Fig. 8), but these apertures are poorly preserved on the skull referred to *Ibidopodia.* This area is missing from the fragmentary skull we found near the articulated skeleton of *Palaelodus.* Occipital fontanelles occur in many other families of birds (Fig. 8), but, except for the Alcidae, which differ from the fossil skulls as stated earlier, there are no salt glands in any of these families. The family Threskiornithidae differs from the fossil remains primarily by having a less convex frontal and an almost completely closed interorbital septum. In the Anatidae, where most species have occipital fontanelles, the frontal is flat and oblique, the interorbital septum is almost closed, and the temporal fossa is present for the entire height of the braincase, but it is very shallow. In the Rostratulidae, Haematopodidae, Charadriidae, and Scolopacidae, the braincase is spheroid, and the parietal is very oblique, almost horizontal, on the posterior face. So, among all the birds with occipital fontanelles above the foramen magnum, the fossil remains bear the greatest resemblance to the flamingo skulls (Fig. 8).

So, if we exclude the Alcidae, from which they differ particularly in the shapes of the frontal and the temporal fossae, the fossil remains are much more similar to flamingo skulls than to those of any other family, especially in the presence of both grooves for salt glands and the apertures above the foramen magnum. These similarities reinforce our assumption that the fragmentary skull we found in the vicinity of the articulated skeleton of *Palaelodus* and the two referred skulls can indeed be attributed to *Palaelodus,* whose postcranial skeleton also shows many similarities with that of flamingos (Cheneval, 1983a, 1983b).

←

Figure 1. *Palaelodus ambiguus.* Referred material. Almost complete skeleton FSL 444220. General view. **cv,** cervical vertebrae; **lf,** left femur; **lh,** left humerus; **lj,** lower jaws; **lm,** left carpometacarpus; **lr,** left radius; **ltb,** left tibiotarsus; **ltm,** left tarsometatarsus; **lu,** left ulna; **p,** pelvis; **rf,** right femur; **rh,** right humerus; **rm,** right carpometacarpus; **rr,** right radius; **rtb,** right tibiotarsus; **rtm,** right tarsometatarsus; **ru,** right ulna. Scale bar = 5 cm.

Figure 2. *Palaelodus ambiguus.* Referred material FSL 444220. Detail of the wing bones. Scale bar = 2 cm.

Figure 3. *Palaelodus ambiguus.* Referred material FSL 444220. Detail of the foot bones. Scale bar = 2 cm.

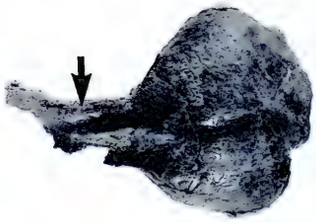

Figure 4. *Palaelodus ambiguus.* Referred material. Fragmentary skull referred to the skeleton FSL 444220. Dorsal view. Note the strong grooves, probably for salt glands (arrow). Natural size.

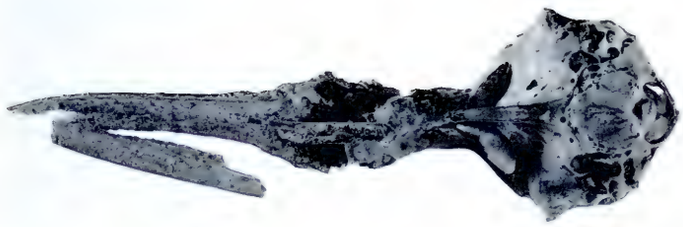

Figure 6. *Palaelodus ambiguus.* Referred material. Skull ML S'G 60 (labeled "*Hidopodia palustris*," *lapsus calami* for *Ibidopodia palustris*). Ventral view. Natural size.

As one of the referred skulls was previously described as a species of the family Gruidae, we can better describe the fossil skull remains in comparison with the skull of flamingos and cranes. In dorsal view (Fig. 7), the frontal differs from the very rounded condition found in cranes, being comparatively more flattened as in flamingos. The anterior part of the frontal is narrow because of the large size of the orbits, which is more similar to flamingos than to cranes. The two salt gland grooves are deeper than those on flamingo skulls, where they are separated by a fine groove, and they lack the lateral ridge along the edge of the orbit. Grooves of this nature do not appear on crane skulls, where the frontal is completely flat in the corresponding area, except in *Balearica* Brisson 1760 where there is a large convexity. In posterior view (Fig. 8), the foramen magnum of the fossil skull is large, with the sides more or less straight lines, whereas it is more rounded in cranes. Above the foramen magnum, the occipital protuberance is only slightly convex between the two apertures; the area is much more convex on the crane skulls. The occipital protuberance is also crossed by a fine lateral protrusion, which is very well marked as in flamingos and which does not exist on crane skulls. The occipital condyle is also rather small, as in flamingos. In ventral view (Fig. 6), the basitemporal plate is rather flat, whereas in flamingos and cranes it is more furrowed. The sphenoidal rostrum is thick, more so than in flamingos and more similar to that of cranes. In lateral view (Fig. 9), the temporal fossa is large and rather deep, which does not resemble either flamingos or cranes, where this fossa is shallower and more confined. The temporal fossa climbs up to the lateral protrusion of the parietal, as in flamingos. The opisthotic fossa is not expanded and is comparatively lower, more similar to that of cranes than to that of flamingos, where it is high and deep. The interorbital septum shows an important upper opening into the braincase, as in flamingos, and also a large lower medial opening, as in cranes.

The bill is very similar to that of flamingos, if we exclude the curved anterior part so typical of the flamingos. In dorsal view (Fig. 7), the premaxillary is short, straight, and fairly large, and its end is rounded. The premaxillary of the fossil species is totally different from that of the cranes, which is long, thin, and very sharply pointed. The nasal, in the dorsal part between the two nostrils, is proportionately a little more slender than in flamingos. In lateral view (Fig. 9), the most important characteristic is the shape of the nostrils; these are longer than in flamingos, but not so much as in cranes. In its general aspect, the bill looks very much like that of the recently described primitive flamingo-like bird *Juncitarsus merkeli* (Peters, 1987:figs. 1, 3).

Contrary to early authors (Gervais, 1848–1852; Milne-Edwards, 1867–1871), we do not think that the skull of *Palaelodus* resembles those of species of the family Anatidae. In the anatids, the frontal is very flat and without grooves, and the foramen magnum is very large. The occipital protuberance is very protruding between the two fontanelles, which are very near one another when they are present, and the entire area is surrounded by a long horseshoe-shaped ridge (Fig. 8). In lateral view, the sphenoidal rostrum is thin, and the basitemporal plate is proportionately larger, more elongated, and fairly curved. The interorbital septum is almost solid with only very small openings. On the spatulate bill, the nostrils are short and rounded, and the lower jaws are very thin. There is only a vague superficial resemblance between the skulls of *Palaelodus* and Anatidae, just as there are some osteological similarities in the postcranial

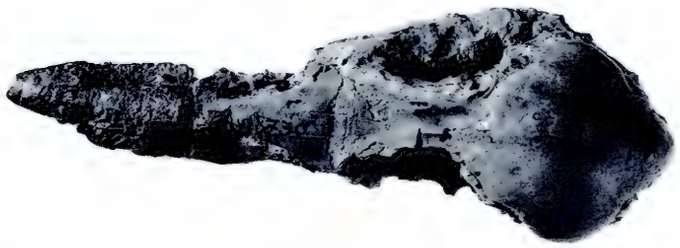

Figure 5. *Palaelodus ambiguus.* Referred material. Skull MNHN Av 8730 (=*Ibidopodia palustris* Milne-Edwards). Dorsal view. Natural size.

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Figure 7. Dorsal view of the skull of some modern birds and *Palaelodus ambiguus.* From top to bottom, *Phoenicopterus ruber, Palaelodus ambiguus* (referred material ML S'G 60), *Grus grus, Pygoscelis papua, Alca torda, Gavia immer, Pachyptila vittata,* and *Larus marinus.* Note the grooves for salt glands, which are totally absent on the skull of *Grus grus.* Natural size.

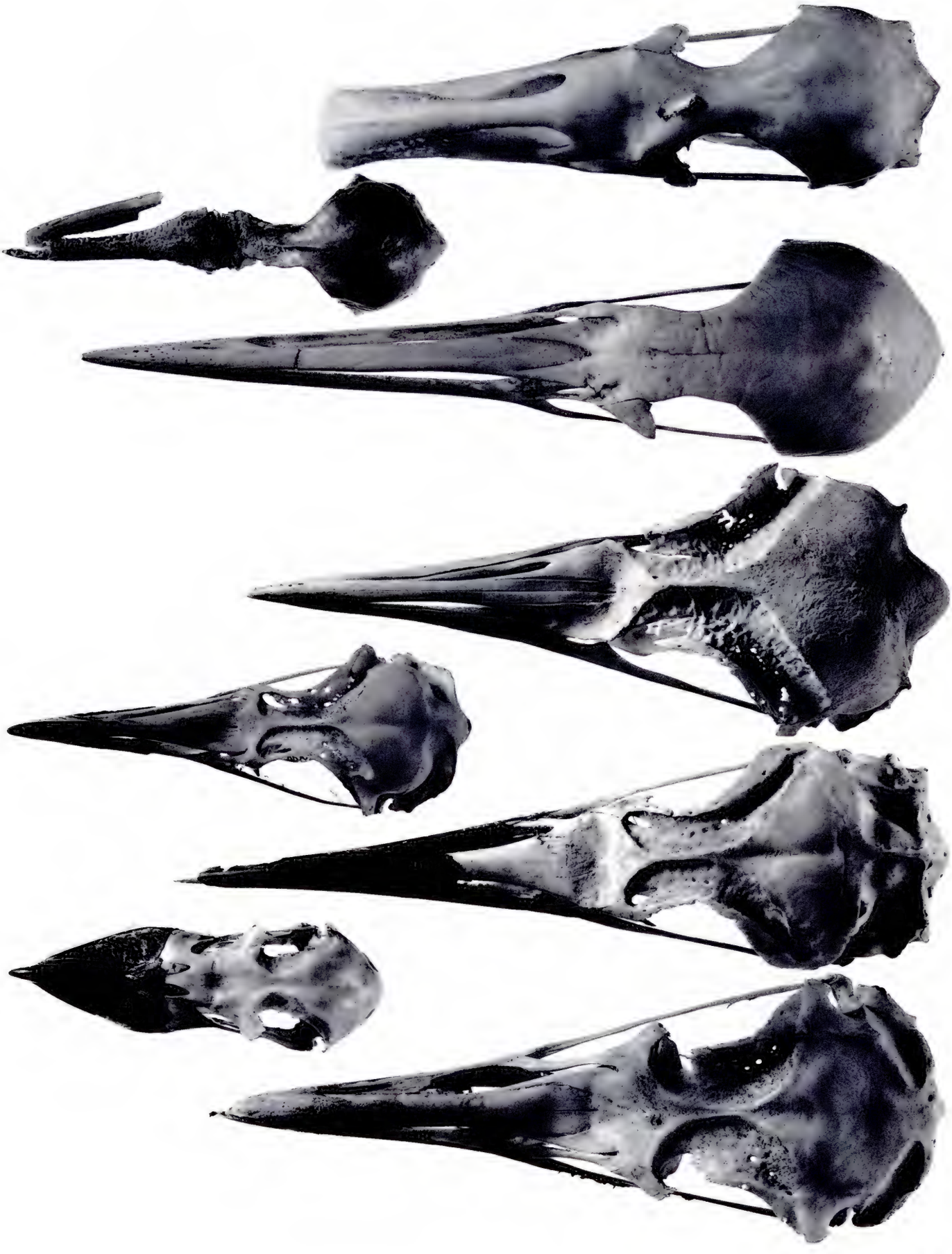

Figure 8. Posterior view of the skull of some modern birds and *Palaelodus ambiguus*. From left to right: top, *Phoenicopterus ruber, Palaelodus ambiguus* (referred material ML S^{t}G 60), and *Grus grus;* below, *Eudocimus albus, Anas platyrhynchos,* and *Recurvirostra avosetta.* Natural size.

skeleton, e.g., disposition of the hypotarsus on the tarsometatarsi, lateral flatness of the tibiotarsi, and form of the distal condyles on the femora (see Cheneval, 1983b).

In comparison with the skull of Recurvirostridae, there are more similarities. However, in the avocets, the frontal is large, with two anterior excrescences and no grooves. The foramen magnum is almost perfectly round and surmounted by two apertures that are very close together, and the occipital protuberance is well developed (Fig. 8). The sphenoidal rostrum is thin. The interorbital septum is almost the same in the two groups. The temporal fossa is deep, as in *Palaelodus,* but on the skull of the avocet it is very narrow, whereas it is wide on the skull of *Palaelodus.* So, in this case too there are resemblances between the skulls just as there are postcranial similarities between the two families (Olson and Feduccia, 1980b; Cheneval, 1983b).

DISCUSSION

ECOLOGICAL CONSEQUENCES

Palaelodids were very unusual, flamingo-like birds unlike any living group. Olson and Feduccia (1980b) considered these birds to have more of a swimming habit than do flamingos and to have occupied a duck-like ecological niche. As previously stated (Cheneval, 1983a, 1983b), we feel these birds were better adapted to diving. Adaptations to diving can be identified with some skeletal modifications. There are three primary types of modifications (Storer, 1971): development of the wings for use under water (three lineages: diving petrels, penguins, and auks), foot-propelled specialization (four lines: cormorants, loons, grebes, and Cretaceous Hesperornithes), and both foot-propelled and wing-propelled divers (diving ducks). According to Storer (1971), foot-propelled diving birds show a long, narrow pelvis, a short femur with a double articulation in the region of the acetabulum (by means of a well-developed trochanter), a long tibiotarsus with a very well-developed cnemial crest, and a laterally compressed tarsometatarsus with a very well-developed hypotarsus. For these characters, foot bones of *Palaelodus* show many similarities with those of a foot-propelled diving bird such as *Podiceps* Latham 1787; on this basis, we interpret palaelodids as having been better diving birds than swimming birds (Cheneval, 1983a).

The description of the palaelodid skulls and of the sparse

Figure 9. Lateral view of the skull of *Phoenicopterus ruber, Palaelodus ambiguus* (referred material ML S'G 60), and *Grus grus* (from top to bottom). Natural size.

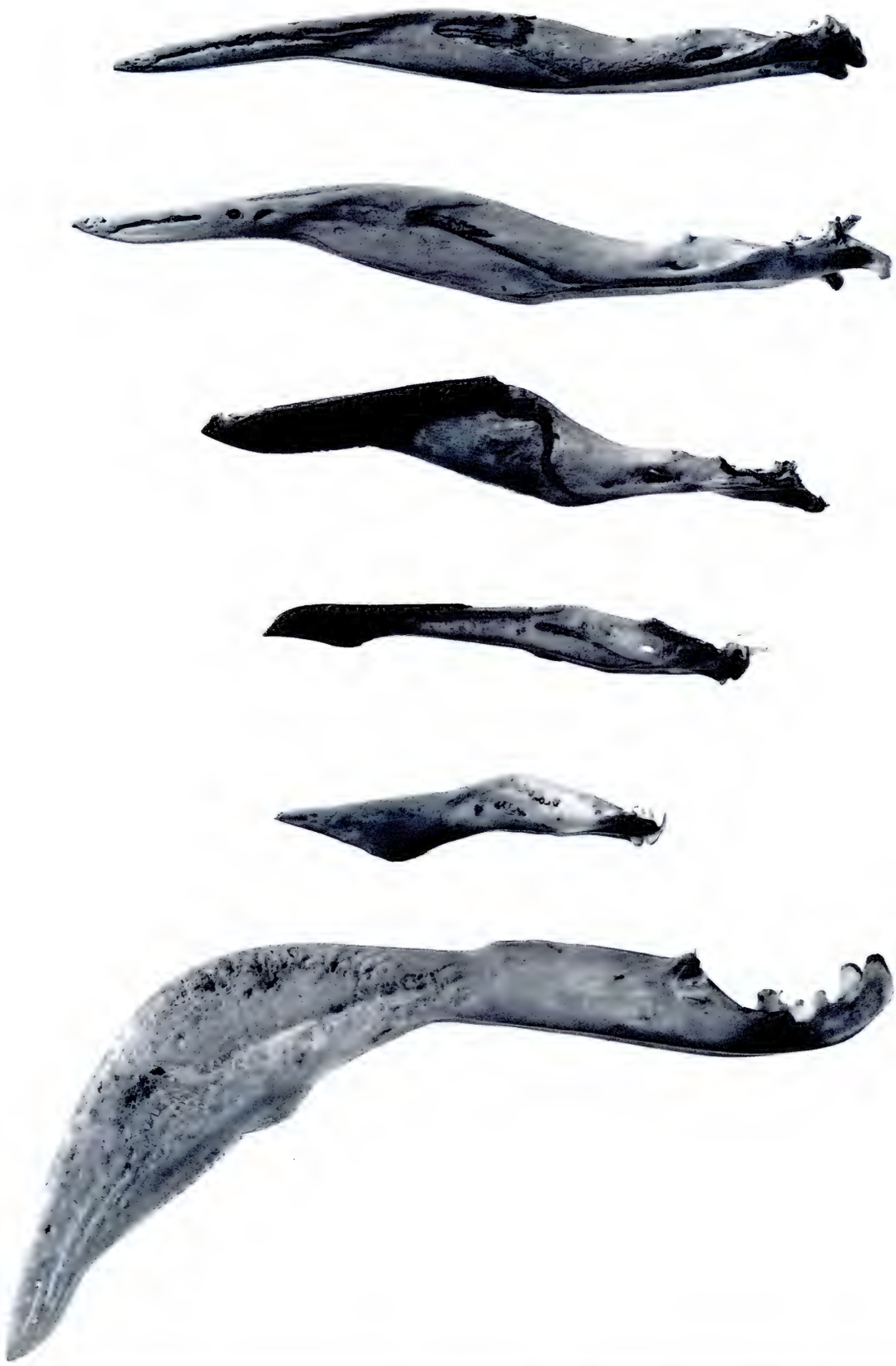

Figure 10. Comparison of the lower jaw of some modern aquatic birds. From top to bottom, *Pygoscelis papua* (I), *Pygoscelis antarctica* (PF), *Eudyptes chrysocome* (PF), *Alca torda* (FF), *Fratercula arctica* (I), *Phoenicopterus ruber* (PF). Abbreviations: FF, fish-feeders; I, intermediate behavior; PF, plankton-feeders. Lateral view. Natural size.

remains of lower jaws now enables us to develop some hypotheses regarding their feeding behavior. Palaelodid birds show many affinities with flamingos, which are highly specialized filter-feeders; thus, one hypothesis could be that palaelodids were also filter-feeders. The evolution of filter-feeding has recently been studied by Olson and Feduccia (1980b). A filter-feeding apparatus, more or less well developed, is employed in five groups of birds. A primitive apparatus appears in plankton-eating species of both auks and penguins (Bédard, 1969; Zusi, 1975) and is characterized by an enlarged tongue and a broadened upper jaw. Modifications associated with an enlarged tongue include either a distensible gular pouch (auks) or a deepening of the lower jaw (penguins). A better developed filter-feeding apparatus is seen in the diving petrels of the genus *Pachyptila* Illiger 1811, which have an enlarged tongue accommodated by a gular pouch and a broadened bill. These two adaptations are also present in the filter-feeding apparatus of diving ducks. But the most specialized filter-feeders are flamingos (Jenkin, 1956–1957). In both flamingo groups, *Phoenicopterus* Linnaeus 1758 on one hand and *Phoenicoparrus* Bonaparte 1856 and *Phoeniconaias* Gray 1869 on the other, the lower jaw is very deep and swollen and forms a large cylinder for an immense tongue. All filter-feeders, except auks and penguins, possess lamellae on the edge of the jaws.

So, a common characteristic for all filter-feeders appears to be an enlarged tongue; concurrently, the bill is often broadened. But it also seems that the height of the lower jaws extends progressively, in its posterior part, with the degree of filter-feeding specialization (Fig. 10). Measurements of the length of the upper jaw and of the greatest height of the mandibles, and values of the ratio between the two measures for some members of aquatic bird groups, are given in Table 2. The ratio is low for groups where there is no filter-feeding behavior, e.g., cranes, with which *Palaelodus* has been compared. (*Balearica* seems to be an exception here because of the shortness of the bill.) In groups where both filter-feeders and nonfilter-feeders exist, e.g., Alcidae and Spheniscidae, our data show this ratio always to be lower for fish-feeder forms than for plankton-feeder ones.

The Alcidae seems to be the most characteristic family for which Bédard (1969) defined three types of feeding behavior: plankton-feeding, fish-feeding, and intermediate, i.e., both plankton- and fish-feeding. For the species we could study (Table 2; Fig. 10), fish-feeders have the lowest ratio (*Alca* Linnaeus 1758, *Uria* Brisson 1760, *Cepphus* Pallas 1769, and *Synthliboramphus* Brandt 1837); the ratio is a little higher for intermediate species *Cerorhinca* Bonaparte 1828 and *Fratercula* Brisson 1760) and is highest for plankton-feeders (*Plautus* Gunnerus 1761, *Ptychorhamphus* Brandt 1837, and *Aethia* Merrem 1788). The same trend seems to be seen for penguins (Table 2), where the ratio is also high. The ratio is a little lower for the primitive bird *Presbyornis* Wetmore 1926, but its value could only be estimated from photos (Olson and Feduccia, 1980a:figs. 8, 9) and should be considered as an indicative value only. No value can be calculated for *Juncitarsus merkeli* Peters 1987 whose bill is in very poor condition. For *Palaelodus*, the ratio has been calculated with bill length of the two complete skulls and the greatest height we could measure on the crushed remains of mandibles on the slab (FSL 444220). This ratio is higher in comparison to flamingos, but it could be overvalued because this fragmentary skull is a little larger than the two complete skulls, raising the possibility that the lower jaws were oversized for the two other skulls. Nevertheless, the height of the mandibles suggests that *Palaelodus* may have already developed a filter-feeding apparatus, which was probably more primitive than in modern flamingos, but perhaps comparable to plankton-feeding auks and penguins.

The last aspect of this discussion is the probable presence in the *Palaelodus* skull of salt glands. This character suggests that palaelodid birds lived near saline lakes and that the lakes of Saint-Gérand-le-Puy were more or less brackish water expanses. This hypothesis has already been demonstrated by the presence of other saline aquatic birds, such as a flamingo, *Phoenicopterus croizeti* Gervais 1848–1852, and also an ibis, *Plegadis paganus* (Milne-Edwards 1867–1871), and a cormorant, *Phalacrocorax littoralis* (Milne-Edwards 1863), whose related modern species can be found preferentially in brackish water expanses (Cheneval, 1983b, 1989).

RELATIONSHIPS AND EVOLUTIONARY CONSEQUENCES

With this description of the skull, we no longer have any doubt that the palaelodids are related to flamingos and have no affinities with cranes. The similarities that their skulls show with those of *Recurvirostra* Linnaeus 1758 and the Anatidae are not surprising, as Olson and Feduccia (1980a, 1980b) have demonstrated the relationships between Charadriiformes, Anseriformes, and Phoenicopteriformes.

Within the flamingo group, *Palaelodus* seems more primitive than modern flamingos in the development of a filter-feeding apparatus, but it is more specialized in its locomotor apparatus. Thus, the *Palaelodus* group may represent an early separate lineage rather than an ancestral group for modern flamingos. The presence in the same deposits of a real flamingo, *Phoenicopterus croizeti* (Cheneval, 1983b, 1984), seems to confirm that the two lineages split from a common ancestor earlier. So, contrary to Olson and Feduccia (1980b), we think it is better to retain the *Palaelodus* and *Megapaloelodus* species as a separate group relative to the flamingos and to the primitive genus *Juncitarsus*, either in their own family (Palaelodidae) if the order Phoenicopteriformes is retained, or in a new subfamily (Palaelodinae) within the Phoenicopteridae if this family is placed in the order Charadriiformes (position of Olson and Feduccia, 1980b). Peters (1987:153) is the first to our knowledge to use the name Palaelodinae.

No evidence indicates the age of the divergence of palaelodids from flamingos. The genus *Juncitarsus* was described from the Middle Eocene of Wyoming (Olson and Feduccia, 1980b) and Germany (Peters, 1987). This genus shows intermediate characteristics between charadriid birds and flamingos, and it is difficult, without a direct comparison, to determine whether *Palaelodus* diverged before or after the appearance of *Juncitarsus*. As currently known, palaelodid birds ranged from the Early Oligocene, based on two species from Egypt related to *Palaelodus* (Olson and Rasmussen, 1986; Rasmussen et al., 1987) to the middle Pleistocene (in northern South Australia; D. Baird and P. Rich, pers. comm.).

Placing the fragmentary bill described by Milne-Edwards (1867–1871) as *Grus* (=*Probalearica*) *problematica* in synonymy with *Palaelodus ambiguus* poses a problem for the genus *Probalearica*. The type species *Probalearica problematica* was described on the basis of this fragmentary bill and two slabs with crushed and fragmentary sterna from the Upper Oligocene deposits of Gannat (Allier, France). One of these slabs is in the collection of the Paris Museum (MNHN Av 8729; figured in Milne-Edwards, 1867–1871:pl. 76, fig. 4); the other is missing (Milne-Edwards, 1867–1871:pl. 76, fig. 3). In his systematic study of the fossil cranes, Cracraft (1973) designated the fragmentary

Table 2. Measurements (mm) and ratio (percent) of skulls for some nonfilter-feeding and filter-feeding birds. FB, feeding behavior (FF, fish-feeders; I, intermediate behavior; NF, nonfilter-feeders; PF, plankton-feeders); LI, length of the upper jaw (*, estimated by means of a line to take into account the great curve of the bill); HJ, greatest height of the lower jaw.

	n	FB	LI	HJ	(HJ/LI) × 100	Means
Gruidae						
Grus grus	2	NF	107.6–117.9	16.5–17.1	13.99–15.89	14.94
Grus canadensis	1	NF	109.6	12.5	11.40	—
Grus vipio	1	NF	149.0	15.7	10.54	—
Grus antigone	1	NF	154.2	18.9	12.26	—
Grus leucogeranus	1	NF	189.0	20.5	10.85	—
Anthropoides virgo	1	NF	78.3	11.0	14.05	—
Balearica pavonina	2	NF	62.0–64.5	12.7–13.3	20.48–20.62	20.55
Spheniscidae						
Pygoscelis papua	1	I	67.6	12.9	19.08	—
Pygoscelis antarctica	1	PF	69.4	16.6	23.92	—
Eudyptes chrysocome	3	PF	54.3–59.4	16.6–18.9	30.57–31.86	31.42
Eudyptes pachyrhynchus	1	PF	51.7	17.5	33.85	—
Alcidae						
Uria aalge	6	FF	53.2–57.8	8.7–10.2	15.40–18.15	16.51
Uria lomvia	2	FF	57.9–58.5	9.8–10.3	16.75–17.79	17.27
Cepphus columba	2	FF	44.3–45.0	7.3–7.9	16.48–17.55	17.01
Cepphus grylle	2	FF	42.2–44.7	7.2–8.3	17.06–18.57	17.81
Alca torda	6	FF	47.5–52.4	8.7–10.4	17.94–20.51	19.15
Synthliboramphus antiquus	1	FF	23.4	4.9	20.94	—
Cerorhinca monocerata	3	I	43.6–49.3	8.6–9.6	17.44–22.02	19.79
Fratercula arctica	4	I	41.1–46.3	8.6–9.5	19.44–22.03	20.85
Plautus alle	1	PF	30.6	5.4	17.65	—
Ptychorhamphus aleuticus	1	PF	23.8	5.0	21.01	—
Aethia pusilla	1	PF	24.1	5.6	23.24	—
Aethia pygmaea	1	PF	29.0	7.0	24.14	—
Procellariidae						
Pachyptila vittata	1	PF	40.6	6.3	15.52	—
Anatidae						
Anas platyrhynchos	15	PF	47.0–58.2	8.6–11.0	16.82–21.32	18.14
Presbyornithidae						
Presbyornis sp.*	1	PF?	50.7	8.6	17.06	—
Phoenicopteridae						
Phoenicopterus ruber	14	PF	138–162*	25.6–31.0	17.30–20.42	19.23
Phoenicoparrus andinus	1	PF	128*	22.9	17.89	—
Palaelodidae						
Palaelodus ambiguus	1	PF?	44.0–46.0	10.2±	22.17–23.18	22.67

* From Olson and Feduccia (1980a:figs. 8, 9).

bill as holotype (in fact, lectotype). The problem becomes more complicated with the description of three other species in the genus *Probalearica*. *Probalearica crataegensis* Brodkorb 1963b, described from the Lower Miocene deposits of the Hawthorne Formation of Florida, USA, based on a distal end of a tibiotarsus, was placed in *Probalearica* only because of its general similarity to modern *Balearica*. Cracraft (1973) pointed out that no significant differences exist between this tibiotarsus and another fossil genus of cranes, *Palaeogrus* Portis 1885. The second species, *Probalearica moldavica* Kurochkin and Ganya 1972, was described from Upper Miocene deposits of Moldavia and the third, *Probalearica mongolica* Kurochkin 1985, from Middle Pliocene deposits of Western Mongolia. Both of these species were also based on the distal end of a tibiotarsus, although a distal end of tarsometatarsus and a quadrate were referred to *P. mongolica*. With the designation of a holotype by Cracraft (1973), and with the present paper, the genus *Probalearica* apparently becomes synonymous with *Palaelodus*. For the remaining material of *Probalearica problematica* and the three other species of *Probalearica*, a new study is needed, and direct comparisons with *Palaeogrus* material from Saint-Gérand-le-Puy deposits will determine whether the two crane genera are synonymous or a new genus must be described for the species of "*Probalearica*" (Cheneval, in prep.).

The synonymy of the skulls previously described as *Ibidopodia palustris* with *Palaelodus ambiguus* poses less of a problem. All the original material for *I. palustris* is in the collection of the Paris Museum (skull MNHN Av 8730; tarsometatarsi

MNHN Av 8731, 8732; figured in Milne-Edwards, 1867–1871: pl. 71, figs. 17–21), and the tarsometatarsus MNHN Av 8731 was designated as holotype by Lydekker (1891). The two genera are thus not synonymous. Until now, no relationships have been demonstrated for *Ibidopodia palustris*, and this bird must remain as *incertae sedis*.

SUMMARY

Flamingo-like birds of the genus *Palaelodus* were first described from the important avifauna of the Saint-Gérand-le-Puy area (Allier, France). For a long time, an exasperating problem was the absence of skulls of these birds, despite the abundance of other remains. The discovery of an almost complete skeleton attributed to *Palaelodus ambiguus* and of a fragmentary braincase found in the immediate vicinity enables us to assert that the skull of these birds was previously described as remains of a fossil crane, *Probalearica problematica*, and an enigmatic species, *Ibidopodia palustris*.

Skull remains of *Palaelodus* are typically characterized by the presence of deep grooves on the interorbital part of the frontal (probably for salt glands), the presence of large occipital fontanelles above the foramen magnum, the great width and deepness of the temporal fossa compared to the flamingo skull, and a relatively straight bill. The major characters of the skull emphasize the affinities of the palaelodids with modern flamingos.

Despite the poor preservation of the palaelodid skull remains, the peculiar height of the lower jaw and a comparison with some modern filter-feeders suggest that palaelodids may have developed a filter-feeding apparatus. However, it was certainly more primitive than the highly specialized apparatus of the modern flamingos.

In our opinion, the *Palaelodus* group and the flamingos split from a common ancestor very early, an interpretation reinforced by the presence in the deposits of Saint-Gérand-le-Puy of a "real" flamingo, *Phoenicopterus croizeti*. However, without direct comparison, it is difficult to determine whether palaelodids diverged from flamingos before or after the appearance of the primitive genus *Juncitarsus*.

An unsolved problem is the position of the remaining material of *Probalearica*. A fragmentary bill has been designated as lectotype of the type species *P. problematica* (Cracraft, 1973); the remaining material of this species is definitely not from a palaelodid species. Three other species were also described from Miocene and Pliocene deposits of the USA and Eastern Europe. A new study is needed, one that also provides direct comparisons with the remains of another crane genus from the Saint-Gérand-le-Puy deposits, *Palaeogrus;* this study will determine if a new genus must be described for the species included within "*Probalearica*."

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A MIOCENE ANHINGA FROM COLOMBIA, AND COMMENTS ON THE ZOOGEOGRAPHIC RELATIONSHIPS OF SOUTH AMERICA'S TERTIARY AVIFAUNA

D. Tab Rasmussen and
Richard F. Kay

ABSTRACT. A cervical vertebra and the distal end of an ulna from the middle Miocene Honda Group of Colombia's Upper Magdalena Valley are referred to the family Anhingidae, and they represent the first fossil record of this family in South America. The specimens are from a large species of *Anhinga* similar in size to *Anhinga grandis* Martin and Mengel 1975 from the upper Miocene of North America. The Colombian anhinga fossils and the extinct hoatzin, *Hoazinoides magdalenae* Miller 1953 from the same deposits, are the only Cenozoic birds from northern South America that predate the Pliocene. The fossil anhinga and hoatzin suggest that the Honda Group was deposited in a tropical lowland with a sluggish river system or swampland bordered by bushes or trees. The Colombian anhinga is additional evidence that suggests significant interchange of volant birds between North and South America prior to the formation of an intercontinental land bridge in the Pliocene.

Key words: Anhingidae, Neotropical avifauna, American biotic interchange, paleoenvironment, bird evolution.

INTRODUCTION

Recent field work in Colombia has yielded two fossil fragments of a large species of anhinga, the first fossil record of the family Anhingidae from South America and only the second pre-Pliocene Cenozoic bird from the northern part of the continent. Most of South America's Tertiary birds have been described from the southern part of the continent, especially Argentina (Campbell, 1979; Rich, 1979; Tonni, 1980). The one exception is *Hoazinoides magdalenae* Miller 1953, based on a single incomplete cranium from the Miocene of Colombia (Fig. 1). The new anhinga specimens described here are thus a significant addition to South America's meager avian fossil record.

The anhinga fossils were recovered from the Miocene Honda Group in Colombia's arid Upper Magdalena Valley, which lies between the eastern and central cordilleras of the Andes. The Honda Group comprises two formations: the lower La Dorada Formation and the overlying Villavieja Formation. The Honda Group is the source of the La Venta Fauna (Stirton, 1953; Hirschfield and Marshall, 1976), which includes a wide variety of fish, reptiles, and mammals (Savage, 1951). The one anhinga fossil for which we have precise locality information is from the Baraya Volcanic Member in the lower part of the Villavieja Formation. This member is composed of thick, extensive, gray to grayish-white sandbodies with pale greenish-gray to brown mudstones and waxy bentonitic claystones (J. Guerrero, pers. comm.; Wellman, 1970). Mammalian faunal correlation suggests a Friasian age (Stirton, 1953; Hirschfield and Marshall, 1976), but three recently published fission-track dates between 14.6 ± 1.1 and 16.1 ± 0.9 Ma (Tekamura and Danhara, 1986) suggest a late Santacrucian age according to a recent revision of these land-mammal ages (Marshall et al., 1986).

Recent expeditions led by personnel from Duke University in cooperation with the Instituto Nacional de Investigaciones Geológico-Mineras (INGEOMINAS) collected vertebrate fossils from the surface at numerous erosional exposures within the extensive badlands area of the Magdalena Valley. Specimens are housed at the INGEOMINAS geological museum (IGM) in Bogotá. The two anhinga specimens are a cervical vertebra and the distal end of an ulna. These elements are usually not particularly valuable for taxonomic purposes, but they are especially distinctive in the family Anhingidae, allowing positive familial identification.

SYSTEMATICS

Family Anhingidae Ridgway 1887

Genus *Anhinga* Brisson 1760

Anhinga sp. cf. *A. grandis* Martin and Mengel 1975

Figures 2, 3

SPECIMENS AND LOCALITIES. (1) IGM 183549, a 13th (or 12th) cervical vertebra, generally well preserved except for the loss of the tips of the hypapophysis, anapophyses, and other delicate crests because of abrasion or breakage (Fig. 2). The specimen was obtained from a local amateur collector in the village of Villavieja, which lies in the La Venta badlands. The Honda Group is almost certainly the source of the fossil, as suggested by the quality of mineralization and the encrusting matrix and by the fact that the fossil mammals in the amateur's collection represent the same species present in the Honda Group. The overlying Miocene Mesa Formation is also exposed near Villavieja, but it is not fossiliferous. (2) IGM 183485, the distal end of a left ulna in excellent condition (Fig. 3). This specimen came from the Fish Bed of Fields (1959) within the Baraya Member of the Villavieja Formation. At this locality the deposits include a bed of an extremely fine-grained, clayey marl ranging

Figure 1. Map of South America showing the position of the La Venta Badlands, Upper Magdalena River Valley, Colombia (star), source of the anhinga specimens described here and *Hoazinoides*. All other pre-Pliocene Tertiary birds described from South America come from the southern part of the continent (shaded area).

from 2 to 6 m thick. This bed contains abundant fish and rodent remains as well as coprolites and other fossil fragments.

CERVICAL VERTEBRA. The cervical vertebrae in the family Anhingidae are highly specialized for sudden stabbing thrusts used for impaling fish on a sharp bill, and they differ considerably from the vertebrae in even their closest living relatives, the families Phalacrocoracidae and Sulidae (Garrod, 1876; Forbes, 1882). Outside the order Pelecaniformes, the closest general, but superficial, resemblance to anhinga vertebrae is found in the family Ardeidae, another group of birds that uses sudden thrusting motions of the neck and head. The Colombian fossil vertebra can be referred to the family Anhingidae by virtue of the following combination of characters: an elongated shape; a relatively expanded cranial end with a ventral tendinal arch and strong hypapophysis and haemapophyses; pre- and postzygapophyses that are displaced far dorsal to the centrum; a pair of strong longitudinal crests on the ventral part of the centrum forming a deep tendinal channel; and the absence of a neural spine.

An anhinga neck consists of three distinct segments: a dorsally convex upper portion (vertebrae 1–9), a dorsally concave middle portion (vertebrae 9–14), and a final segment with slight dorsal convexity (vertebrae 15–20). The fossil vertebra can be identified as belonging to the middle segment by the characters previously listed, especially the presence of paired longitudinal crests on the ventral part of the centrum. In life, these crests house the tendons of m. longus colli ventralis, which is largely responsible for sudden thrusts of the neck. The 14th vertebra differs from the others of the middle segment by lacking a complete ventral channel. Vertebrae 9–13 are similar to each other morphologically, but they show reduced length and increasing robustness caudally. In these respects, and in the presence of robust bases for the anapophyses, the fossil vertebra most closely resembles the 13th vertebra. It could, however, be the 12th vertebra because it is much larger than the vertebrae of modern anhingas and therefore perhaps proportionally more robust as a result of allometric scaling.

The fossil vertebra differs from the 12th and 13th vertebrae of *Anhinga anhinga* mainly in the following features: larger size; rounder, less elongated articular surfaces of the prezygapophyses; ventral channel relatively shallower and broader at its caudal end; and less pronounced lateral cresting pattern on the cranial end (although this may be partly a result of abrasion of the fossil).

Measurements. Length of centrum, 26.3 mm; midline caudal height, 11.3 mm; breadth across prezygapophyses, 15.9 mm; and breadth across postzygapophyses, 14.4 mm. Comparable measurements for centrum length and caudal height (mean ± 1 standard deviation) for eight specimens of *Anhinga anhinga* vertebrae (in the collections of the Duke University Department of Zoology and the U.S. National Museum, Smithsonian Institution) are as follows: centrum length, 17.1 ± 0.92 mm; and caudal height, 8.18 ± 0.48 mm.

DISTAL ULNA. The fossil ulna can be assigned to the family Anhingidae and distinguished from all other bird families by the following combination of characters: distal extension of the internal condyle well beyond the trochlear surface; deep square-cut notch between the internal condyle and the carpal tuberosity; margin of the outer condyle that smoothly joins the ulnar shaft without abrupt angles or notches; absence of pneumaticity; and the presence of paired, moderately developed feather papillae, the anconal row stronger than the inner row.

The fossil ulna differs from that of *Phalacrocorax* Brisson 1760 (Phalacrocoracidae) by having a smaller internal condyle that does not extend as far in the palmar direction and a more square-cut notch between the internal condyle and carpal tuberosity. The fossil ulna differs from that of *Morus* Vieillot 1816 (Sulidae) in having a smaller, squared-off carpal tuberosity, a greater distal extension of the internal condyle, a lack of pneumatic fossae and foramina, a deeper and less broad radial depression, and by lacking a strongly defined tendinal groove. The fossil ulna differs from that of extant *Anhinga anhinga* by having a larger size, a less prominent internal condyle, and weaker papillae.

Measurements. Maximum breadth from the tip of the carpal tuberosity to the opposite margin of the external condyle, 12.4 mm; maximum depth of external condyle, 10.0 mm; breadth and depth of shaft at base of trochlea, 7.7 and 5.3 mm, respectively. The comparable measurements (mean ± 1 standard deviation) of eight *Anhinga anhinga* ulnae are as follows: maximum breadth, 10.56 ± 0.25 mm; condyle depth, 7.72 ± 0.32 mm; and breadth and depth of shaft, 6.21 ± 0.30 and 4.83 ± 0.17 mm, respectively.

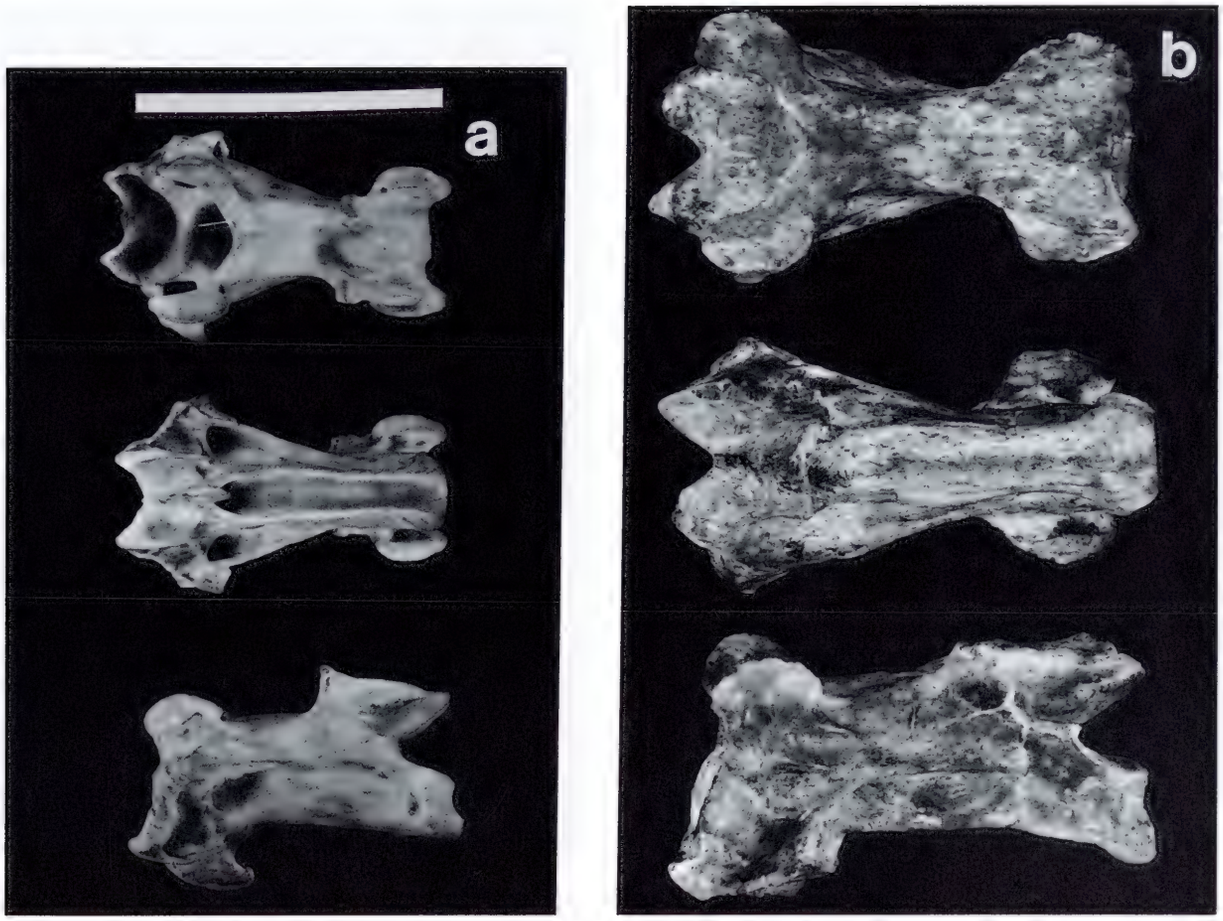

Figure 2. Thirteenth cervical vertebrae of anhingas in dorsal (top), ventral (middle), and left lateral (bottom) view. **a.** *Anhinga anhinga.* Scale bar = 20 mm. **b.** IGM 183549, *Anhinga* sp. cf. *A. grandis* from Colombia (delicate processes broken off). Scale same as in **a.**

REMARKS. Because the two specimens are probably from the same deposits and are of compatible size, they most likely represent a single species. No features of the cervical vertebra or the ulna are sufficient to distinguish either from the corresponding bone in the genus *Anhinga.* The two specimens are much larger than the corresponding bones of any known species of *Anhinga,* except for *A. grandis* and possibly an undescribed Pliocene species from Libya (Becker, 1986). The fossil vertebra and ulna fall within the general size range expected for these elements in *A. grandis.* The humerus of North American *A. grandis* is about 20–40 percent larger in most linear dimensions than that of *A. anhinga* (Martin and Mengel, 1975; Becker, 1986, 1987), whereas measurements of the vertebra and ulna from the Honda Group average about 43 and 20 percent larger, respectively, than the corresponding measurements in *A. anhinga.*

DISCUSSION

The Colombian anhinga is the second avian fossil reported from the Miocene deposits of the Upper Magdalena Valley. The other species, *Hoazinoides magdalenae,* is known only from the holotype cranium that was recovered from the same deposits as the new anhinga specimens. The cranium of *Hoazinoides* closely resembles that of modern *Opisthocomus* Illiger 1811 (Miller, 1953). Olson (1985b) noted that the extinct *Hoazinoides* occurs west of the Eastern Cordillera, whereas modern hoatzins live only east of the Andes. *Hoazinoides* thus represents the first record of the family outside the Amazon–Orinoco drainage. However, fossil fishes suggest that during deposition of the Honda Group the Upper Magdalena Valley was confluent with the Amazon or Orinoco Basins, not the northward-draining Magdalena River as today (Lundberg et al., 1986). Recent *Anhinga anhinga* is broadly distributed in tropical, lowland rivers of South America and occurs in both the Amazon and Lower Magdalena river systems.

Tertiary birds from South America that belong to living families should prove to be especially valuable in paleoenvironmental reconstructions because many South American mammalian taxa do not have living descendants to use as analogues. Recent anhingas are freshwater divers that subsist almost entirely on fish. Living anhingas and hoatzins commonly nest in trees that overhang slow rivers, ponds, or swamps, suggesting that such a habitat existed in the area of the Magdalena Valley during deposition of the Honda Group, a conclusion consistent with other components of the fauna such as crocodilians and the diverse, forest-dwelling, cebid monkey fauna. Modern anhingas generally must launch themselves into flight from trees or bushes, because take-off from water is difficult or impossible for them (Owre, 1967).

Fossil anhingas have been reviewed by Olson (1985b) and Becker (1986, 1987). The Colombian anhinga represents the first

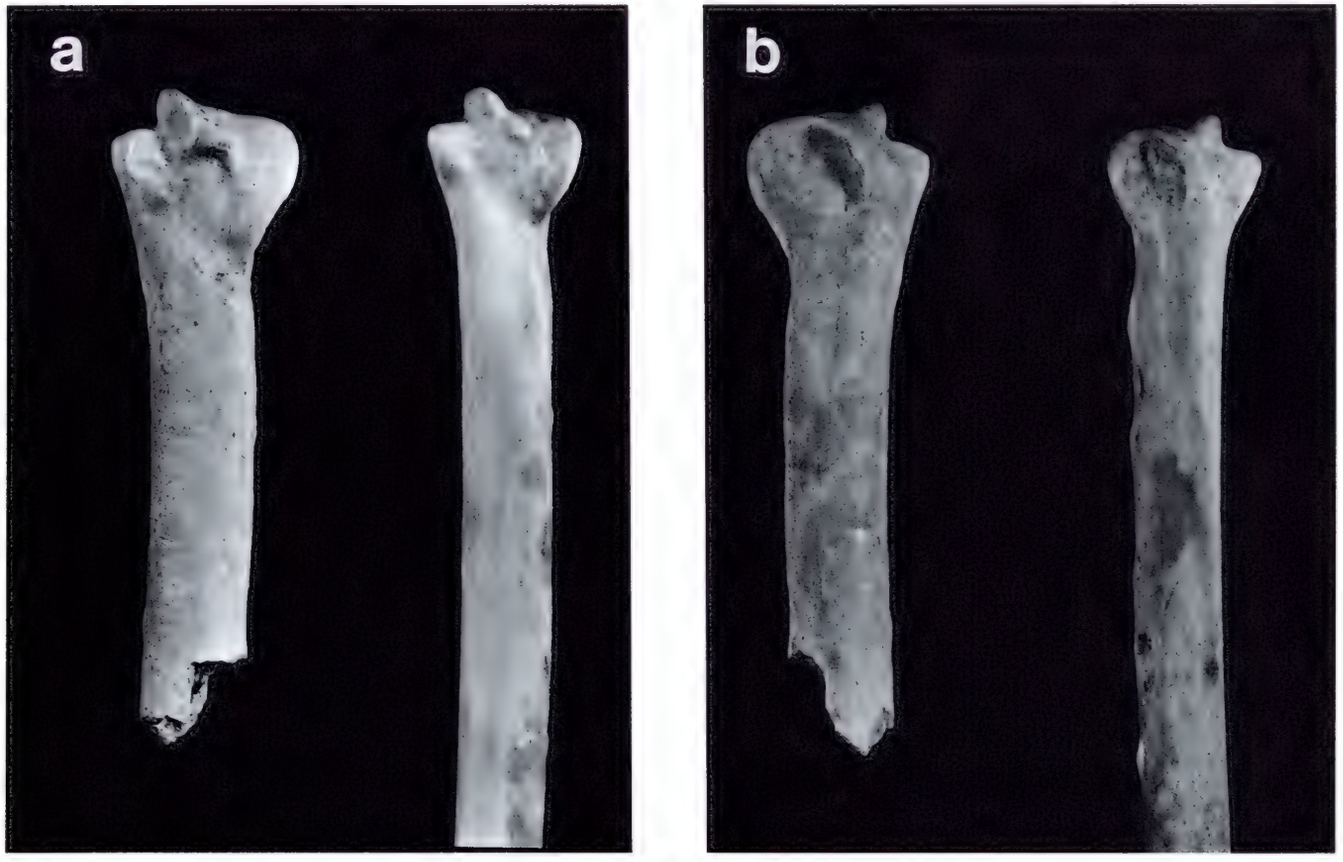

Figure 3. Distal ends of left ulnae. **a.** Internal views of IGM 183485, *Anhinga* sp. cf. *A. grandis* (left) and *A. anhinga* (right). **b.** External views of same specimens. Length of the fossil specimen is 44.5 mm.

fossil record of the family Anhingidae in South America, although Miocene anhingas were previously known from Africa, Europe, and North America. Lambrecht (1916) named *Anhinga pannonica* from Hungary on the basis of a 6th cervical vertebra and a carpometacarpus. Rich (1972) assigned a 7th cervical vertebra and the proximal end of a humerus from the Beglia Formation of Tunisia to the same species. These fossil 6th and 7th vertebrae come from the first dorsally convex section of the neck and differ markedly from vertebrae in the following dorsally concave segment, thus making direct comparison with the Colombian specimen impossible. *Anhinga pannonica* apparently resembled modern *A. rufa* in size and in having more slender and elongated cervical vertebrae than *A. anhinga*. The cervical vertebra of the Colombian anhinga is larger than that of *A. pannonica* and comparable in proportions to *A. anhinga*. Two Miocene species are known from North America; the large *A. grandis,* based on a distal humerus from Nebraska and with referred specimens from Florida (Becker, 1987), and the smaller *A. subvolans,* known from the proximal end of a humerus from Florida (Martin and Mengel, 1975; Becker, 1986), which is the oldest known member of the family with an approximate age of 18 Ma (Becker, 1986). The Colombian specimens are late Santacrucian or Friasian in age, or approximately 14–16 Ma, and predate all known records except *A. subvolans. Anhinga pannonica* and *A. grandis* are both from the late Miocene (Becker, 1986, 1987). Thus, the Colombian anhinga, if it proves to be referable to *A. grandis,* predates the North American records for the species.

The occurrence of a species of *Anhinga* in the Miocene of South America adds to evidence that shows notable Tertiary contact between the avifaunas of South America and those of other continents, especially North America (Martin, 1983). Vuilleumier (1985) disagreed with the hypothesis that much interchange had occurred, concluding that the avifaunas of North and South America were apparently isolated from each other from the Eocene through the Miocene and that extensive interchange between the continents did not occur until the Pliocene, as was the case for mammals. This conclusion was obtained from a generic-level analysis of the North and South American avifaunas, which found that 99 percent of North American genera and 97 percent of South American genera were restricted to their respective continents during the Eocene, Oligocene, and Miocene, a much higher rate of endemism than occurs among the modern avifaunas of North and South America. However, Vuilleumier's analysis of fossil genera probably exaggerated the dissimilarities of the two continental faunas for the following reasons: (1) the rarity of fossil birds from sites in northern South America and southern North America prohibits comparison of the areas where the greatest resemblances between the continents would be expected, as in the living avifaunas; (2) comparison of paleoavifaunas from the very few bird-producing sites in South America does not take into account temporal and paleoenvironmental mismatches with fossil bird localities in North America, i.e., if localities were precisely contemporaneous and represented identical paleoenvironments, then they would probably have more genera in common; (3) Tertiary

Table 1. Distribution of bird families known from pre-Pliocene Tertiary deposits in South America.[a]

Strictly South American before the Pliocene	Known from other continents before the Pliocene
Rheidae	Anhingidae
(+ Opisthodactylidae)	Presbyornithidae
Opisthocomidae	Ciconiidae
Teratornithidae	Accipitridae
Cladornithidae	Falconidae
Cunampaiidae[b]	Phorusrhacidae
Onychopterygidae[b]	Pelecanidae[b]
	Anatidae[b]
	Gruidae (+ Aramidae)[b]

[a] Compiled from Tonni (1980) and Vuilleumier (1984, 1985), excluding seabirds as in Vuilleumier (1984); also following, in part, Patterson and Kraglievich (1960), Cracraft (1973), Mourer-Chaviré (1981), and Olson (1981; 1985a, 1985b).

[b] Taxa based on isolated, damaged, or poorly studied material that some authors consider to be of questionable or no validity (Tonni, 1980; Olson, 1985b).

birds may be oversplit at the generic level, and many genera from South America are dubious because of insufficient material or study (Olson, 1985a; Vuilleumier, 1987).

A family-level comparison of North and South American bird faunas, although not free of methodological problems, does provide sure evidence of faunal exchanges between North and South America (Table 1). It must be noted that the precise number of avian families present in the Tertiary of South America is not agreed upon by those studying South American fossils, and this uncertainty is expressed to some extent in Table 1. However, the exclusion of dubious taxa or inclusion of some additional families by splitting does not alter the following general conclusions. Of 15 Tertiary non-marine families identified in South America before the completion of a land bridge between the continents, nine are present in North America or Europe during the same time span, whereas the remaining six families are unique to South America. Members of the South American family Rheidae are flightless. Fossil remains for the flightless family Phorusrhacidae have been reported from pre-Pliocene deposits outside South America (Mourer-Chauviré, 1983; Peters, 1987). The family Cladornithidae is known from a lone distal end of a tarsometatarsus of a large bird that may or may not have been flightless. The family Opisthocomidae includes a single extant species that is a notoriously poor flier unlikely to attempt crossing a substantial water barrier. Nothing is known of the flight capacities of the extinct and poorly known genera *Cunampaia* Rusconi 1946 and *Onychopteryx* Cracraft 1971, each of which has been assigned to its own family (but see Olson, 1985a).

In contrast, eight of the nine families (88.9 percent) of pre-Pliocene South American birds known to be proficient fliers are present in North America well before the formation of a land connection. The one exception is the family Teratornithidae, represented in the Miocene of South America by a volant species but not recorded in North America until the Pliocene (Campbell and Tonni, 1980). Thus, the geographic separation of North and South America during the Tertiary may not have had an appreciable effect on the dispersal of volant bird families. Four of the South American families (Accipitridae, Gruidae, Ciconiidae, and Anhingidae) are also known from African Oligocene or Miocene localities (Rich, 1972; Rasmussen et al., 1987). *Anhinga* becomes the second Tertiary genus, along with *Presbyornis* Wetmore 1926, that is known to occur in both South America and elsewhere before the Pliocene. Based on the limited number of bird taxa currently identified from South America, many South American bird groups, unlike mammals, apparently did not evolve in "splendid isolation" but, rather, experienced significant interchange with other continents. Only the recovery and identification of many additional bird taxa can clarify the full extent of South America's relationships to other continents, the direction of interchange, and which continents were most important in the pre-Pliocene exchanges.

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NEW RECORDS OF MIDDLE MIOCENE ANSERIFORM BIRDS FROM KERN COUNTY, CALIFORNIA

Hildegarde Howard

ABSTRACT. Previously unreported anseriform bones from the Middle Miocene Sharktooth Hill Bonebed in Kern County, California, reveal the presence of a large species with adaptations for diving not evidenced in the previously described *Presbychen abavus* Wetmore. The new form is described, on the basis of four specimens, as *Megalodytes morejohni* new genus, new species. The remaining specimens are discussed as *Megalodytes* sp. and Anseriformes spp. An ulna previously referred to *Branta* sp. is included in the latter category. *Megalodytes morejohni* appears to have been a swan-like anserine, whereas *Presbychen abavus* was a goose-like bird.

Key words: anseriforms, Miocene, California, Sharktooth Hill.

INTRODUCTION

The Middle Miocene Sharktooth Hill Bonebed is a rich fossil deposit in the upper part of the Round Mountain Silt, which crops out in Kern County, California (see Mitchell, 1965:fig. 1). This bonebed is exposed near the Kern River, approximately 13–16 km northeast of Bakersfield, and it has yielded the most diverse and best-studied Tertiary fossil marine vertebrate assemblage known from anywhere within the Pacific realm (Mitchell, 1966; Barnes, 1976; Barnes and Mitchell, 1984). The fossil assemblage has been named the Sharktooth Hill local fauna (Wood et al., 1941), and it comprises more than 100 species of sharks, bony fish, turtles, birds, and mammals, including rare fossils of some terrestrial mammals, reptiles, and birds that originated from the adjacent Miocene land mass. Some of the fossils to be described in this report were derived from outcrops of the bonebed adjacent to the Sharktooth Hill National Natural Landmark, as established by the National Park Service in 1976.

The Sharktooth Hill Bonebed is a single, relatively thin, but laterally widespread horizon. It has been correlated with the Barstovian North American Land Mammal Age, and with the "Temblor" provisional provincial mega-invertebrate stage of Addicott (1972) and is, therefore, between approximately 13 and 15 Ma (Wood et al., 1941; Mitchell, 1966; Barnes, 1976; Barnes and Mitchell, 1984:4).

Avian fossils are rare in this deposit, but those found are in a relatively good state of preservation, even when interspersed amid larger, sometimes broken and abraded bones of mammals and other vertebrates. Fifteen avian taxa were previously reported from the Sharktooth Hill local fauna by Howard (1984). These included two large anseriform birds: *Presbychen abavus* Wetmore 1930 and *Branta* sp. (Miller, 1961). The latter record is based on a single proximal end of an ulna in the collections of the University of California, Museum of Paleontology, Berkeley (UCMP 95970).

The holotype of *Presbychen abavus* is the distal end of a right tibiotarsus in the United States National Museum (USNM 11973). As described by Wetmore (1930:93), the specimen is "strongly suggestive of the modern Canada Goose," and "intermediate in dimension between the largest of the Canada geese and the whistling swan." Over 30 years later, the species was again cited from the Sharktooth Hill local fauna (Howard, 1966) with the assignment of a proximal end of a tarsometatarsus and, questionably, a fragmentary proximal end of a femur. Both of these specimens are in the collections of the Natural History Museum of Los Angeles County (LACM 16466 and 16465).

In the early 1970s, Dr. G. Victor Morejohn of the California State University, San Jose, was studying the Sharktooth Hill anseriform material in the collections of the University of California, Museum of Paleontology, Berkeley. In a letter to me dated 25 March 1974, he indicated that he interpreted the proximal end of a humerus (UCMP 93050) to be in several ways more similar to that of the fossil diving duck, *Chendytes* L. Miller 1925, than to the geese or swans. He added that a proximal fragment of tibiotarsus on loan to him from the Natural History Museum of Los Angeles County (LACM 34530) was also suggestive of *Chendytes*.

Fourteen anseriform bones are now known from the Sharktooth Hill Bonebed, including the previously recorded material (Wetmore, 1930; Miller, 1961; Howard, 1966), the bones noted by Morejohn, and an additional eight specimens not previously studied. Among the latter is a nearly complete tibiotarsus (LACM 123991) collected in 1982 from LACM locality 4956, near the Sharktooth Hill National Natural Landmark. This specimen provides the opportunity to compare the distal end with the holotype of *Presbychen abavus*. The comparison clearly indicates distinction, with the proximal end showing characters associated with the diving anseriforms. Very closely associated in the same quarry were two femora (LACM 123992 and 123993) and a fragment of a humerus (LACM 123995) of a large diving anseriform. The present paper provides a description of a new genus and species based on this material. The possible relationship of other Sharktooth Hill anseriform specimens to this new genus is discussed.

Figure 1. Anserine tibiotarsi: *Presbychen abavus,* holotype, USNM 11973; **A,** posterior view; **B,** internal view; **C,** anterior view; *Megalodytes morejohni,* holotype, LACM 123991; **D,** anterior view; **E,** posterior view; **F,** internal view; *Megalodytes* sp.; **G,** UCMP 93052, distal end, anterior view; **H,** UCMP 93051, proximal fragment, anterior view.

METHODS AND MATERIALS

Acronyms used for institutions housing specimens are as follows: LACM, Natural History Museum of Los Angeles County, Los Angeles, California; UCMP, University of California, Museum of Paleontology, Berkeley; and USNM, United States National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Anseriform material now available from Sharktooth Hill is as follows.

Recorded Material. *Presbychen abavus* Wetmore 1930: holotype (cast) distal end of tibiotarsus, USNM 11973; referred proximal end of tarsometatarsus, LACM 16466 (Howard, 1966); referred proximal end of right femur, LACM 16465 (Howard, 1966). *Branta* sp. (Miller, 1961), proximal end of ulna, UCMP 95970.

Material Examined by Morejohn (Unrecorded). Proximal end of right humerus, UCMP 93050, loc. V71013; proximal end of left tibiotarsus, LACM 34530, loc. 1625.

Additional Unrecorded Material. Nearly complete left tibiotarsus, LACM 123991, loc. 4956; nearly complete left femur, LACM 123992, loc. 4956; nearly complete right femur, LACM

123993, loc. 4956; incomplete left femur LACM 123994, loc. 4956; proximal fragment of right humerus, LACM 123995, loc. 4956; proximal end of right humerus, LACM 122979, loc. 3162; left tarsometatarsus lacking distal end, LACM 122981, loc. 3162; proximal and distal fragments of right tibiotarsus, UCMP 93051 and 93052, loc. V71013.

The 50 skeletons of modern anseriforms used for comparison are in the collections of the Natural History Museum of Los Angeles County and include 12 specimens of the genus *Cygnus*, 10 of *Branta*, eight of *Anser* plus eight representatives of the tribe Mergini and one or more of each of the other tribes recognized in the *American Ornithologists' Union Check-list of North American Birds* (American Ornithologists' Union, 1983).

SYSTEMATICS

Order Anseriformes (Wagler 1831)

Family Anatidae Vigors 1825

Subfamily Anserinae Vigors 1825

Tribe Cygnini

Megalodytes new genus

DIAGNOSIS. A large anserine having tibiotarsus with distal extension of inner cnemial crest projecting beyond medial edge of shaft and extending distad below level of proximal terminus of fibular crest; anterior surface of shaft very slightly rounded (nearly flat); distinguished from holotype of *Presbychen* Wetmore 1930 by greater breadth than depth of condylar area and supratendinal bridge tilted posteriad along its proximal border; and distinguished from holotype of *Chendytes* L. Miller 1925 by less distal extension of inner cnemial crest, less flattened anterior face of shaft and less flared fibular crest.

TYPE SPECIES. *Megalodytes morejohni* new species.

ETYMOLOGY. The generic name, *Megalodytes*, is derived from Greek; *megalo-* (*megas*), meaning large, and *dytes*, meaning diver; masculine.

Megalodytes morejohni new species

Figures 1D–F, 2, 3A, D

HOLOTYPE. Left tibiotarsus with eroded proximal surface and incomplete cnemial crests, LACM 123991. Collected by Samuel A. McLeod, 8 May 1982.

DIAGNOSIS. As for genus.

REFERRED SPECIMENS. Proximal fragment of right humerus, LACM 123995; left and right femora, nearly complete, LACM 123992 and 123993.

TYPE LOCALITY AND HORIZON. LACM locality 4956, quarry grid sections 3-D,-E,-H, Round Mountain Silt, Sharktooth Hill Bonebed, Kern County, California; Middle Miocene.

ETYMOLOGY. The species is named in honor of Dr. G. Victor Morejohn.

MEASUREMENTS (mm) OF HOLOTYPE. With comparable measurements of *Presbychen abavus* in parentheses: length, 151.9; breadth of distal end, 18.3 (18.6); internal depth of distal end, 16.6 (19.0); breadth of incomplete proximal end, 16.8; and breadth from cnemial crest to fibular crest, 14.6.

DESCRIPTION. The holotype tibiotarsus, LACM 123991, and the femora, LACM 123992 and 123993, were found within a few meters of one another in the quarry. At the time of collection, they appeared to belong to one individual, and their size, shape, preservation, and stage of maturity certainly do not contradict this idea. There is, however, no way to prove the association positively; thus, the femora can only be referred to *Megalodytes morejohni*.

Both the tibiotarsus and the femora resemble those of the genus *Cygnus* Bechstein 1803 in the stoutness of the shaft. Positions of the ligamental and flexor attachments on the posterior face of the tibiotarsus and the relatively greater breadth than depth of the distal end are suggestive of the condition in *Cygnus olor* (Gmelin 1789). The anterior face of the shaft is, however, flatter, and the extension of the inner cnemial crest is more flared medially and of greater distal extent, suggesting greater diving ability.

The femora resemble those of *Cygnus* in the nearly straight shaft, when viewed anteriorly, which is greater in lateral breadth than in anteroposterior depth. Distally the popliteal area is deeper than in *Cygnus* or in *Branta* Scopoli 1769, but less sharply defined than in *Mergus* Linnaeus 1758. The fibular condyle extends laterad slightly proximal to the external condyle, suggestive of the condition in the diving ducks of the tribe Mergini, but it is less abruptly protruded. In species of the Mergini, the shaft is more curved and relatively greater in depth than in breadth. Compared to the proximal fragment of a femur (LACM 16465), which was tentatively referred to *Presbychen* (Howard, 1966), the head is less proximally projected.

Measurements (mm) of the referred femur, LACM 123993 (the more complete of the two femora) are as follows: length from neck to distal edge of rotular groove, 75.4 (same as in LACM 123992); external length, 81.0; breadth of distal end, 22.6; depth of trochanter, 15.2; breadth at middle of shaft, 9.5; and depth at middle of shaft, 8.5.

The characters of the referred humerus, LACM 123995, are discussed with those of humeri UCMP 93050 and LACM 122979 under *Megalodytes* sp.

DISCUSSION. In reporting the distal end of a femur (LACM 123994) of a large, Middle Miocene, diving anatid from Orange County, California, Howard and Barnes (1987) postulated a relationship to the species represented by this Sharktooth Hill anseriform material. Having now studied the specimen from Orange County in more detail, the following characters serve to distinguish it from the femora of *Megalodytes morejohni*: greater anteroposterior than lateral breadth of shaft, more abrupt protrusion of the fibular condyle, and popliteal area more clearly defined externally as well as internally. These characters suggest closer affinity of the Orange County femur to the tribe Mergini than is evidenced by the femora of *M. morejohni*.

cf. *Megalodytes* sp.

Figures 1G, H; 3B, C, E, F

REFERRED SPECIMENS. Proximal shaft fragment (UCMP 93051) and incomplete distal end with shaft (UCMP 93052) of right tibiotarsi and proximal ¾ of right humerus (UCMP 93050) all from UCMP locality V71013; proximal fragment of right humerus (LACM 122979) from locality LACM 3162, Sharktooth Hill Bonebed.

DISCUSSION. The distal end of the tibiotarsus (UCMP 93052) resembles that of the holotype of *Megalodytes morejohni* in the posteriorly tilted position of the supratendinal bridge; the proximal portion of tibiotarsus UCMP 93051 suggests the same faintly rounded anterior surface of the shaft found in the holotype of *M. morejohni*. As the condylar area is incomplete both laterally and anteroposteriorly in UCMP 93052, the relative breadth to depth of the distal end cannot be measured. In breadth at the level of the supratendinal bridge, and breadth from fibular

Figure 2. *Megalodytes morejohni,* referred femora: LACM 123993, right; **A,** posterior view; **B,** external view; **C,** anterior view; LACM 123992, left; **D,** posterior view; **E,** eternal view; **F,** anterior view.

to cnemial crests, UCMP 93052 and 93051 are approximately 9 percent narrower than the holotype of *M. morejohni:* breadth at level of bridge, UCMP 93052, 13.3 mm (in holotype *M. morejohni,* 14.5 mm); breadth from fibular to cnemial crests, UCMP 93051, 13.5 mm (in holotype of *M. morejohni,* 14.6 mm).

Humerus UCMP 93050, from the same locality as the tibiotarsal fragments, has a capital shaft ridge that is less acute and more lateral in position than in *Branta.* Resemblance is closer to humeri of *Cygnus* in the position of the crest, although it is not as prominent as in the swan. This is true, as well, of humerus LACM 122979. In both humeri, also, the head is not undercut by the capital groove. This character, as well as the presence of the capital shaft ridge, distinguishes these specimens from the humeri of the diving ducks (tribe Mergini). Suggestive of the condition in the extinct *Chendytes* is the abrupt palmad receding of the deltoid crest just distal to the external tuberosity and its sharp reduction after a brief flare. This area is eroded in UCMP 93050, but the outline of the shaft suggests the same characters.

In the fragment of humerus (LACM 123995) referred to *Megalodytes morejohni,* the palmar position and reduced size of the deltoid crest (where preserved) and the seemingly lateral position of the capital shaft ridge are strongly suggestive of the condition observed in UCMP 93050 and LACM 122979. The only comparable measurement possible on all three specimens is breadth of shaft just distal to the deltoid crest. This shows a size ratio close to that observed between the tibiotarsi referred to *Megalodytes* sp. and the holotype of *M. morejohni.* Breadth of shaft, LACM 122979, 11.5 mm; UCMP 93050, 11.7 mm; *M. morejohni,* LACM 123995, 12.8 mm.

The similarity of the deltoid crest in humerus UCMP 93050 and LACM 122979 to that of LACM 123995, as well as the similarities noted in the tibiotarsi, justify assignment of this material to the genus *Megalodytes.* Considering the small difference in size, the possible referral of this material to *M. morejohni* should be considered.

Anseriformes spp.

REFERRED SPECIMENS. Incomplete left femur, LACM 123994, from locality LACM 4956 (quarry grid section 10); proximal end of left tibiotarsus, LACM 34530, from locality LACM 1625; incomplete left tarsometatarsus, LACM 122981, from locality LACM 3161; proximal end of ulna, UCMP 95970, from locality UCMP V6323 [assigned by Miller (1961) to *Branta* sp.]; all from Sharktooth Hill Bonebed.

DESCRIPTION. Femur LACM 123994 is poorly preserved, lacking complete proximal and distal ends. Although similar in overall size to the femora referred to *Megalodytes morejohni,* it has greater anteroposterior than lateral breadth of shaft, and the popliteal area, although less deeply depressed than in *M. morejohni,* is more sharply defined externally by a longer ridge. Both of these femoral characters suggest possibly even greater adaptation for diving than is seen in the femora of *M. morejohni.*

The proximal fragment of tibiotarsus (LACM 34530) has the medially flared distal continuation of the internal cnemial crest characteristic of the divers, possibly to an even greater distal extent relative to the size of the bone than in the holotype of *Megalodytes morejohni.* However, it resembles that specimen in the position of the rugosities marking the muscle attachments on the posterior side. Measurements show the specimen to be even smaller than tibiotarsus UCMP 93051 listed herein as *Megalodytes* sp.: breadth from fibular to cnemial crests, LACM 34530, 12.5 mm; UCMP 93051, 13.5 mm.

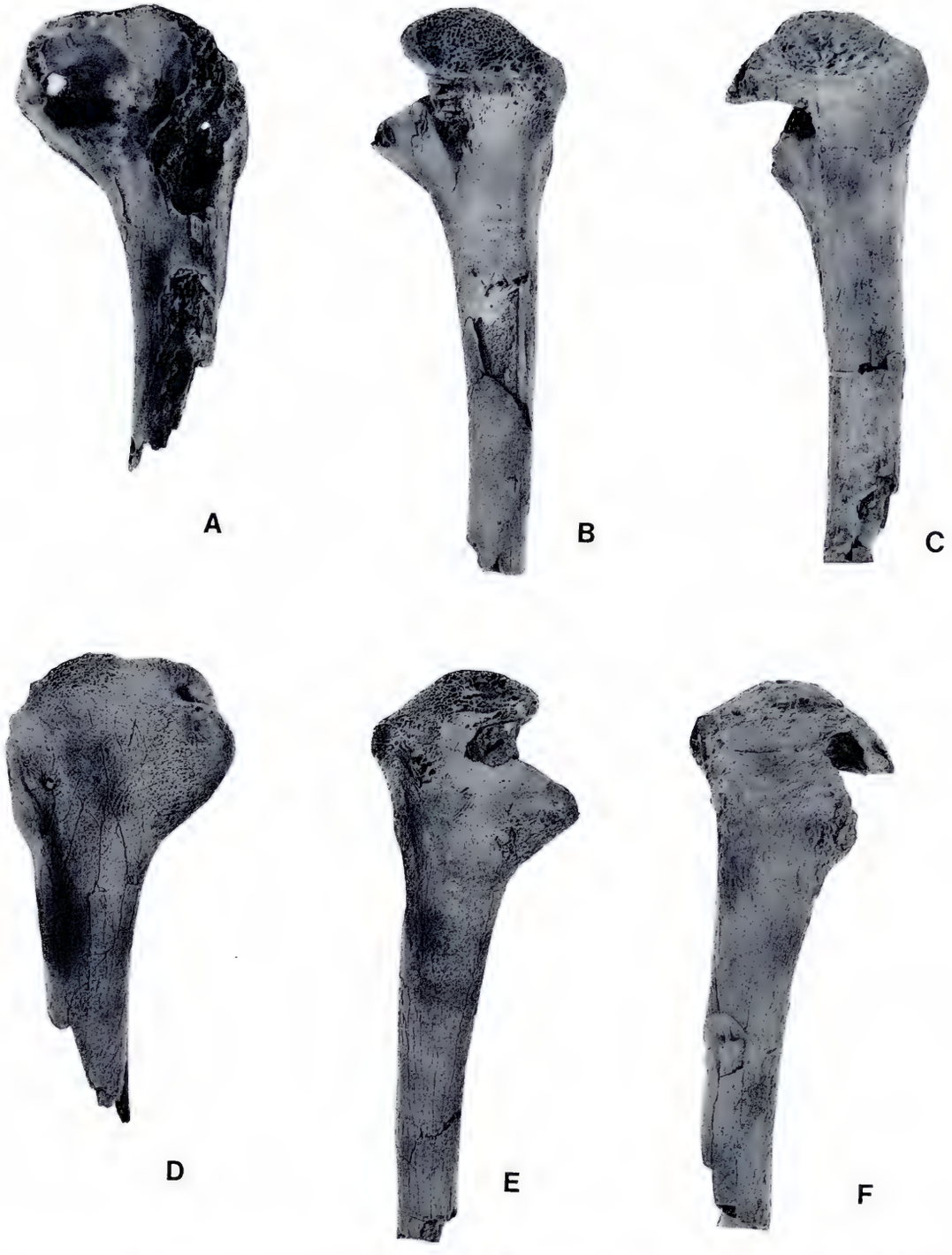

Figure 3. *Megalodytes* humeri: **A–C,** anconal views; **D–F,** palmar views; **A, D** *Megalodytes morejohni,* LACM 123995; **B, E,** cf. *Megalodytes* sp., LACM 122979; **C, F,** cf. *Megalodytes* sp., UCMP 93050 (37 mm of incomplete shaft of 93050 not shown).

Tarsometatarsus LACM 122981 has a long internal calcaneal ridge, even longer than in *Cygnus* and notably longer than in members of the tribe Mergini. The specimen is markedly distinguished from the tarsometatarsus of *Cygnus* by the abrupt narrowing of the internal side of the shaft anteriorly, immediately below the proximal end, and the gradual diminution in breadth (while retaining its depth) toward the distal end. This abrupt narrowing of the shaft is particularly noteworthy in distinction to the proximal end of tarsometatarsus (LACM 16466) previously identified (Howard, 1966) as *Presbychen abavus.* A much narrower metatarsal shaft is characteristic of diving forms such as the grebes and loons.

The proximal end of an ulna that Miller (1961) assigned to *Branta* sp., noting that it was too small to be assigned to *Pres-*

bychen, is similar in size to large specimens of *B. canadensis* (Linnaeus 1758), but with both olecranon and shaft markedly straighter. The high, straight olecranon is suggestive of the condition in *Melanitta* Boie 1822, but the straight shaft more closely resembles that of *Cygnus*.

Were it not for the occurrence of femur LACM 123994, which clearly represents a diver distinct from *Megalodytes morejohni*, these specimens might well have been assigned to *Megalodytes*.

DISCUSSION. Only one other Miocene anseriform species, *Branta howardae* L. Miller 1930 (see Howard, 1983), has been described from California. The species is based on a single distal fragment of carpometacarpus from the Upper Miocene Dove Spring Formation (originally named Ricardo Formation and considered Lower Pliocene in age) in the Mojave Desert, Kern County, California. There are no carpometacarpi among the Sharktooth Hill specimens with which to compare this specimen, and Miller (1961) made no reference to it when discussing the ulna that he identified as *Branta* sp. from the latter locality.

Three other anseriform species have been described from earlier Miocene deposits in North America: *Paranyroca magna* A. Miller and Compton 1939, *Dendrochen robusta* A. Miller 1944, and *Anas integra* A. Miller 1944. All of these are Early Miocene in age and from Bennett County, South Dakota. *Paranyroca* is known only from two tarsometatarsi, for which the authors established a new "distinctive and primitive anseriform family," the Paranyrocidae, which they said "may have some special phylogenetic relation with the Nyrocinae" (Miller and Compton, 1939:154). The holotype of *Dendrochen robusta* is a humerus that Miller placed in the tribe Dendrocygnini. The medial placement of the capital shaft ridge and the strong undercutting of the head by the capital groove distinguish the specimen from the humeri assigned here to *Megalodytes*. *Anas integra*, placed in the subfamily Anatinae, is known from a coracoid (the holotype) and an ulna. Both specimens clearly represent a small anatine duck that is obviously not related to *Megalodytes*.

CONCLUSIONS

In studying the material discussed herein, it became clear that at least two extinct Middle Miocene species of large anseriform birds are present in the Sharktooth Hill local fauna, namely *Presbychen abavus* and *Megalodytes morejohni* new genus, new species. It is impossible to determine from the material available whether or not the smaller specimens herein identified only as cf. *Megalodytes* sp. represent a separate species.

Whereas *Presbychen* appears to have been a goose-like bird, *Megalodytes* was more like the swans, although with additional adaptations for diving. The temptation was strong to list this new genus under the Mergini. I felt, however, that the observed adaptations for diving were secondary. Or, perhaps, we may postulate that ancient swans had greater diving ability, which has gradually diminished through time.

Of the 14 anseriform specimens now known from Sharktooth Hill, four do not readily fall within either of the above genera and should best be classified only as Anseriformes spp.

In summary, the anseriform specimens from Sharktooth Hill are identified as follows (numbers of specimens in parentheses).

Order Anseriformes
  Family Anatidae
    Subfamily Anserinae
      Tribe Cygnini
        Genus *Megalodytes* (7)
      Tribe Anserini
        Genus *Presbychen* (3)
  Anseriformes spp. (4)

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I want, also, to express my thanks to staff of the United States National Museum of Natural History for providing a cast of the holotype of *Presbychen abavus* and of the University of California, Museum of Paleontology, Berkeley, for the loan of the specimen assigned by Miller to *Branta* sp. and specimens now assigned to *Megalodytes* sp. Some of the LACM specimens were collected from the Sharktooth Hill Bonebed during field operations supported by National Science Foundation Grant No. EAR 79-16508.

I am especially grateful to Pierce Brodkorb of the University of Florida who, when I met with difficulty in finding a scientific name not already in use for a diving bird of large size, came up with the suggestion of *Megalodytes*.

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CROWNED CRANES (GRUIDAE: *BALEARICA*) IN THE MIOCENE OF NEBRASKA

Alan Feduccia and
Michael R. Voorhies

ABSTRACT. A remarkable death assemblage of hundreds of well-preserved fossils, including entire skeletons of rhinoceroses, horses, and camels, was preserved in a bed of volcanic ash of the lower upper Miocene (upper Clarendonian) of Nebraska. Among these skeletons were found numerous partially articulated skeletons of a new, small species of crowned crane, *Balearica,* described herein as a new species, *Balearica exigua.* Evidence indicates a grasslands habitat with standing water, similar to that inhabited by living species of *Balearica* in Africa.

Key words: crowned cranes, *Balearica,* Miocene, Nebraska.

INTRODUCTION

Some 10 million years ago, a volcanic eruption, perhaps more than 100 times greater than that of the recent Mount St. Helens eruption, laid down an ash fall over several hundred square kilometers. This volcanic ash, which reached a depth of 3 m in places, preserves a remarkable death assemblage of vertebrates. The source of the ash fall is thought to have been centered in the area of New Mexico, some 1040 km from the study site (Voorhies, 1985).

The Miocene death assemblage was discovered near the town of Orchard, Antelope County, Nebraska, in a 2-m-thick bed of pure volcanic ash (Voorhies, 1971, 1981, 1985; Voorhies and Thomasson, 1979). It was first excavated by M.R.V. in 1977. The deposits are upper Clarendonian (lower upper Miocene) in age and form part of the Cap Rock Member of the Ash Hollow Formation. Remains of the short-limbed rhinoceros *Teleoceras major* Hatcher 1894 are the most commonly occurring fossils, with approximately 100 skeletons. Horses, camels, and other large vertebrates were also found and by the late fall of 1979, when bulldozers filled in the excavation, Voorhies and his crews had extracted more than 200 skeletons (weighing approximately 40 tons and consisting of 2,000 lots of jacketed fossils). Evidence from both the vertebrates and the plant fossils indicated a warm savanna, with standing water, closely approximating the present-day habitat of African Crowned Cranes.

The predominant avian fossils in the ash deposit were cranes of the genus *Balearica* Brisson 1760. Several dozen individuals of this crane are estimated by M.R.V. to have been preserved at the locality. However, most were sandwiched between the skulls or other parts of the rhinos and other large mammal fossils and were therefore not recovered. Some specimens are preserved with ossified tendons (particularly tibiotarsal and tarsometatarsal), trachael rings, and even some feather impressions. Other bird fossils recovered from the locality include a tern (currently under study), a hawk of the genus *Buteo* Lacépède 1799 [close in size to *Buteo jamaicensis* (Gmelin 1788)], and a hawk that appears to be convergent on the modern African secretarybirds *Sagittarius* Hermann 1783 (Feduccia and Voorhies, 1989). In this paper, we describe the new species of crowned crane and its paleoecological significance.

METHODS AND MATERIALS

The African Crowned Crane [*Balearica pavonina* (Linnaeus 1758)] consists of four subspecies, *B. p. pavonina, B. p. ceciliae, B. p. gibbericeps,* and *B. p. regulorum,* which are distributed over much of the African continent south of the Sahara Desert. *Balearica pavonina regulorum* (with *B. p. gibbericeps*) is often treated as a separate species or semispecies, recognized primarily by slight differences in color markings and bare skin areas or wattles of the head and neck; the southern forms, *B. p. regulorum* and *B. p. gibbericeps,* average slightly larger but overlap *B. p. pavonina* and *B. p. ceciliae* in size. Specimens from Uganda show intergradation between *B. p. cecilae* and *B. p. gibbericeps* (Walkinshaw, 1964). Adult males and females of the species are similar and are characterized by a large, spectacular straw-yellow crown of stiff feathers emanating from the rear of the head. Recently, Snow (1978) and Dowsett and Dowsett-Lemaire (1980) concluded that the crowned cranes should be conspecific (for a discussion of this problem, see Johnsgard, 1983). In this paper, we recognize one living species.

D. Scott Wood provided us with the raw measurements for 10 skeletons each of the two forms of *Balearica* that he utilized in his phenetic study (Wood, 1979), and we have kept the measurements separate in Table 1. The fossil cranes described herein differ significantly in size from the modern species of *Balearica,* being approximately ¼th to ⅛th smaller, so morphometric data are given only as a general reference. Moreover, the fossils are sufficiently different morphologically from the living species so as not to warrent close morphometric comparison with the latter. The slow rate of growth observed for Crowned Cranes poses another problem in identification of fossil forms. Pomeroy (1980) observed a very slow rate of growth and subsequent attainment of adult form in seven Crowned Cranes raised in captivity to 23 months, where weight increase followed a sig-

Table 1. Measurements of two living subspecies of *Balearica pavonina, B. p. pavonina* and *B. p. regulorum,* and the Miocene *Balearica exigua.* Data for the modern forms from Wood (pers. comm. 1979), taken after the method of Schnell (1970). Data are given as mean ± standard deviation; the range is given below in parentheses. Measurements of *Balearica exigua* are also expressed as a percentage of the combined mean of the measurements for the living *Balearica.* Abbreviations: S(l), skull length; PMX (l), length of premaxilla; PMX(ln), length of premaxilla from narial opening; MB(l), length of mandible; MB(d), depth of mandible; CO(l), length of coracoid; SC(w), width of scapula at proximal end; H(l), length of humerus; H(lt), length of trochanter of humerus; H(wd), width of distal end of humerus; R(l), length of radius; CR(l), length of carpometacarpus; CR(d), depth of carpometacarpus; D3P1(l), length of digit III, phalanx 1; D3P1(d), depth of digit III, phalanx 1; CA(l), length of carina (from posterior medial margin of sternum to anterior edge of junction of the two halves of the furcula; CA(d), depth of carina; CM, costal margin; SYN(l), anterior synsacrum length; SYN(w), width of synsacrum across acetabulae; SYN(wm), minimum width of synsacrum; F(l), length of femur; F(wp), proximal width of femur; F(wm), minimum width of femur shaft; F(wd), width of distal end of femur; TB(l), length of tibiotarsus; TB(w), width of shaft of tibiotarsus; TM(l), length of tarsometatarsus; TM(ws), width of shaft of tarsometatarsus; TM(wt), width across trochleae.

	Balearica p. pavonina	*Balearica p. regulorum*	Fossil	Percentage of mean of living *Balearica*
S(l) (estimated)	118 ± 6.49 (107.9–129.5)	116 ± 6.22 (104.8–126.8)	80.0	0.68
Pmx(l)	60.85 ± 3.59 (53.5–65.2)	59.2 ± 3.60 (54.7–65.5)	45.8	0.76
Pmx(ln)	24.36 ± 2.32 (20.9–26.7)	23.19 ± 2.58 (17.1–26.4)	15.8	0.66
MB(l)	102.80 ± 5.85 (91.5–112.4)	99.48 ± 6.36 (88.2–111.1)	71.3	0.70
MB(d)	13.62 ± 0.94 (12.2–15.2)	13.02 ± 0.85 (11.7–14.3)	8.1	0.61
CO(l)	77.92 ± 9.32 (66.5–96.8)	71.36 ± 6.23 (62.3–79.8)	52.0 (n = 4) (48.5–55.8)	0.78
SC(w)	21.24 ± 1.16 (19.1–23.1)	20.63 ± 1.01 (19.1–22.0)	16.6	0.79
H(l)	198.63 ± 7.75 (189.2–228.9)	196.85 ± 9.04 (186.4–211.1)	149.5 (n = 3) (144.7–155.1)	0.76
H(lt)	58.67 ± 3.70 (53.4–64.5)	57.61 ± 2.66 (53.8–61.4)	149.5	0.85
H(wd)	29.45 ± 1.89 (25.5–32.0)	28.46 ± 2.63 (24.5–32.2)	25.6 (n = 2) (25.0–26.2)	0.88
R(l)	215.85 ± 11.86 (198.4–236.4)	207.75 ± 11.68 (192.3–226.2)	169.8	0.80
CR(l)	96.24 ± 4.92 (89.6–106.0)	92.78 ± 4.67 (86.9–100.9)	82.2 (n = 5) (77.4–86.0)	0.87
CR(d)	13.30 ± 0.73 (12.1–14.7)	12.97 ± 0.97 (11.5–14.0)	11.5 (n = 3) (10.6–12.8)	0.88
D3P1(l)	42.36 ± 2.08 (38.9–45.5)	40.45 ± 2.79 (35.2–44.8)	34.0	0.82
D3P1(d)	12.76 ± 1.03 (11.2–15.2)	12.21 ± 0.63 (11.0–13.3)	10.7	0.86
CA(l)	139.71 ± 11.8	137.43 ± 11.18	117.5	0.85
CA(d)	45.42 ± 4.96 (38.9–56.2)	43.31 ± 3.36 (37.4–49.0)	40.8(?)	0.91
CM	54.20 ± 3.00 (n = 8) (50.7–59.6)	50.44 ± 3.02 (46.6–55.8)	34.8	0.67
SYN(l)	85.06 ± 4.72 (78.1–90.0)	86.12 ± 4.36 (78.1–90.0)	65.8	0.76
SYN(w)	48.61 ± 2.99 (42.6–52.7)	49.99 ± 4.55 (43.9–58.8)	30.9(?)	0.77
SYN(wm)	33.83 ± 2.15 (31.8–37.8)	33.22 ± 2.20 (30.1–36.8)	24.6	0.73
F(l)	108.22 ± 5.05 (102.7–118.2)	105.98 ± 5.15 (99.0–112.3)	80.2	0.75

Table 1. Continued.

	Balearica p. pavonina	*Balearica p. regulorum*	Fossil	Percenage of mean of living *Balearica*
F(wp)	23.82 ± 1.76 (20.9–26.3)	23.68 ± 1.81 (21.3–26.6)	17.0	0.71
F(wm)	9.43 ± 0.74 (8.2–10.6)	9.36 ± 0.53 (8.8–10.1)	7.4 (n = 2) (6.9–7.8)	0.79
F(wd)	23.72 ± 1.54 (20.8–26.0)	23.26 ± 1.41 (21.1–25.5)	18.5 (n = 2) (17.2–19.7)	0.79
TB(l)	286.26 ± 11.94 (n = 9) (267.8–302.8)	273.30 ± 15.67 (252.7–298.7)	151.0 (estimate from 2 specimens)	0.54[a]
TB(w)	8.68 ± 0.50 (n = 9) (8.0–9.4)	8.50 ± 0.48 (7.7–9.2)	7.2 (n = 2) (6.9–7.4)	0.84
Tm(l)	206.76 ± 10.89 (188.5–228.9)	202.95 ± 20.17 (175.5–227.3)	125.3 (n = 4) (117.4–131.6)	0.61
TM(ws)	7.64 ± 0.82 (6.3–8.8)	7.42 ± 0.84 (6.0–8.8)	7.15 (n = 2) (6.9–7.4)	0.95
TM(wt)	23.6 ± 2.00 (20.8–26.4)	22.78 ± 1.22 (20.2–24.6)	14.8	0.64

[a] Probably underestimated because one fossil individual was very small.

moid curve, and full adult size was attained at approximately 2 years (breeding is normally at 3 years). In contrast to Sandhill Cranes [*Grus canadensis* (Linnaeus 1758)], which at 4–5 months had attained 91 percent of adult weight (Miller and Hatfield, 1974), Crowned Cranes of that age had attained less than 60 percent of adult weight (Pomeroy, 1980). Indeed, in terms of skeletal characteristics, A.F. has never dealt with an avian species that exhibited as much individual size variation as observed in the crowned crane. Applying the standards of most studies of avian paleontology, it would not be an overstatement that each skeletal specimen of *Balearica* would qualify as a new fossil species, some as distinctive genera!

Among the fossil specimens studied, six are partly articulated skeletons, on slabs, two of which are somewhat complete. Preservation, however, is poor, and most of the bones are incomplete, precluding measurements. Consequently, composite measurements are used in the morphometric comparisons. Modern species studied include the following: *Balearica pavonina*, *Grus grus* (Linnaeus 1758), *G. canadensis*, *G. americana* (Linnaeus 1758), *G. antigone* (Linnaeus 1758), *G. rubicunda* (Perry 1810), *G. monacha* (Temminck 1835), *Anthropoides paradisea* (Lichtenstein 1793), *A. virgo* (Linnaeus 1758), and *Bugeranus carunculatus* (Gmelin 1789). Specimen numbers refer to the University of Nebraska State Museum (UNSM).

SYSTEMATICS

Order Gruiformes (Bonaparte 1854)

Family Gruidae Vigors 1825

Genus *Balearica* Brisson 1750

DIAGNOSIS. Cranes of the genus *Balearica* are morphologically distinctive within the Gruidae and are often placed in their own subfamily Balearicinae (Brodkorb, 1967). They differ from all other genera of cranes by having the following characters. Trachea simple and relatively straight, not convoluted; sternum simple, not accommodating tracheal components. Furcula separate and free from sternum; not ankylosed to keel. Twenty cervical vertebrae. Bill relatively short and simple, not ending in a sharp, pointed tip. Cranium relatively large, exhibiting a bulbous, inflated frontal region that expands anteriorly over the nasal-frontal hinge and exhibits two lateral projections posteriorly. Humerus with pneumatic fossa less excavated and with pneumatic foramen smaller than in Gruinae. Deltoid crest not extending down shaft as in Gruinae and bicipital surface relatively less extensive. Tibiotarsus with internal cnemial crest less developed, shaft relatively more robust and with less internal distal curvature, and distal end anteroposteriorly flattened with medial condyle outwardly rotated. Tarsometarsus shorter with shaft more robust and with trochleae relatively more enlarged. Internal and external trochleae relatively more developed with respect to the middle trochlea and internal trochlea with less posterior projection.

Balearica exigua new species

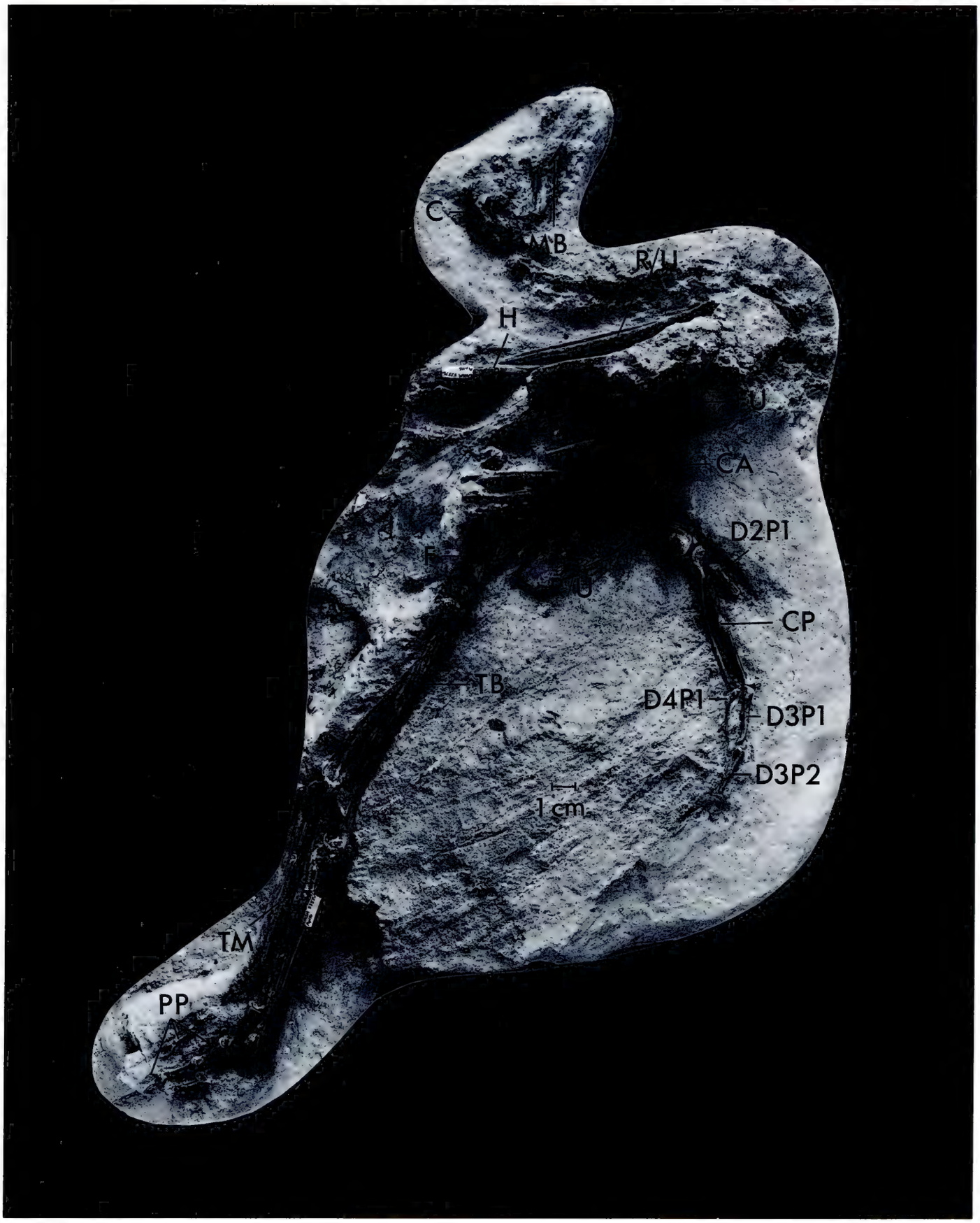
Figures 1–5

HOLOTYPE. Nearly complete, flattened, partially articulated skeleton, but many elements badly crushed. University of Nebraska State Museum 53576 (Fig. 1). Collected by M.R. Voorhies and field party, summer 1978.

DIAGNOSIS. A small crane of the genus *Balearica*, approximately ¼th to ⅛th smaller than the only other known species of the genus, *Balearica pavonina*.

TYPE LOCALITY. Near the town of Orchard, Antelope County, Nebraska, in a 2-m-thick bed of pure volcanic ash at the center of NE¼ NE¼ of NW¼ of Sec. 8, T28N, R7W, 42°20′N, 98°14′W.

TYPE HORIZON AND AGE. Cap Rock Member, Ash Hollow Formation, upper Clarendonian (lower upper Miocene).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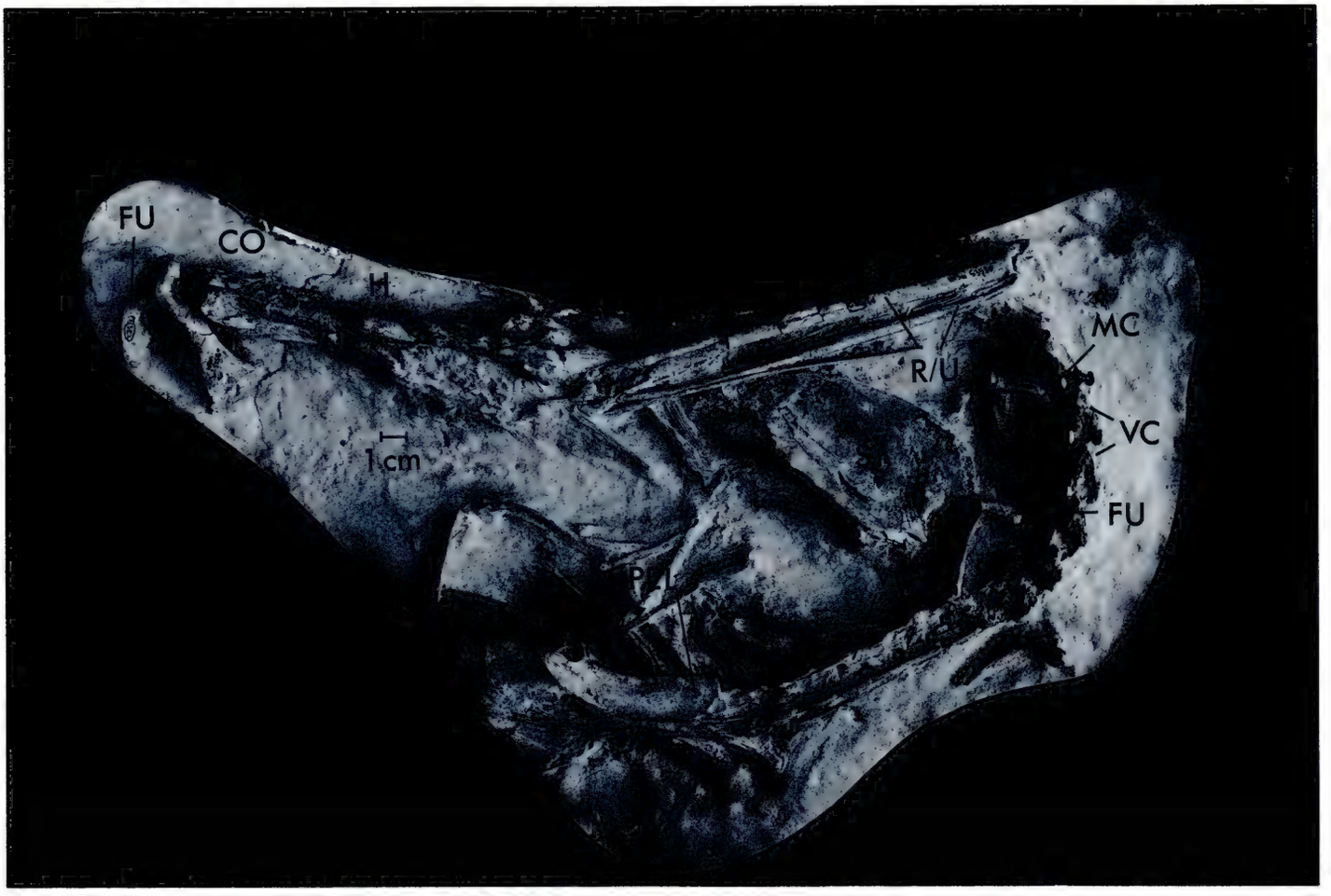

Figure 2. Paratype, partially articulated skeleton of *Balearica exigua* new species, UNSM 53580. Abbreviations same as in Fig. 1 and: **CO,** coracoid; **MC,** mammalian centrum; **PEL,** pelvis; **ST,** sternum; **VC,** vertebral column. Note that the presence of two furculae indicates two individuals present on slab. The wing and associated elements probably do not belong to the same individual as the pelvis and vertebral column.

PARATYPES. UNSM 53580, partially articulated skeleton (Figs. 2, 3); UNSM 53579, skull (Fig. 4) and tarsometatarsus (Fig. 5); and single elements (Figs. 5, 6): UNSM 96734, right humerus; UNSM 96735, proximal end of left tibiotarsus; UNSM 96736, distal end of right tibiotarsus; UNSM 53579, right tarsometatarsus; UNSM 96737, left carpometacarpus; UNSM 96738, left coracoid; UNSM 96739, right digit three phalanx one; UNSM 96740, right radius; UNSM 96741, right ulna; UNSM 23579, left femur. All paratypes are from the same locality as the holotype.

ETYMOLOGY. From Latin, *exigua,* meaning small, little.

MEASUREMENTS. Although abundant remains were recovered, most of the bones were crushed to some extent or otherwise damaged, often with ends crushed or destroyed. Therefore, it was extremely difficult to obtain a large number of accurate measurements. The holotype (UNSM 53576) was so designated because of the articulated nature of the specimen on the slab; however, it provided a very limited set of measurements. Individual elements designated as paratypes often provided the only accurate measurement for a particular element. Measurements (mm) of the holotype are given first where possible, followed by measurements of the paratypes and other elements.

Table 1 gives the range, means and standard deviations for skeletal elements of the two modern forms of *Balearica* recognized by Wood (1979) and measurements from the fossil species *Balearica exigua.* The percentage of the size of the fossil element to the mean of the two subspecies of living *B. pavonina* for which data are available is given to indicate the approximate size of the fossil in relation to living Crowned Cranes. The mean percentage of the fossil elements to modern *Balearica* is 0.77 (standard deviation = 0.10), indicating that the fossil species was 20–25 percent smaller than living *B. p. pavonina* and *B. p. regulorum,* with relatively shorter legs.

←

Figure 1. Holotype skeleton of *Balearica exigua* new species, UNSM 53576. Abbreviations: **C,** cranium; **CA,** carina of sternum; **CP,** carpometacarpus; **D2P1,** digit II, phalanx 1; D3P1, digit III, phalanx 1; **D3P2,** digit III, phalanx 2; **D4P1,** digit IV, phalanx 1; **F,** femur; **FU,** furcula; **H,** humerus; **MB,** mandible; **PP,** phalanges of pes; **R/U,** radius/ulna; **TB,** tibiotarsus; **TM,** tarsometatarsus.

Figure 3. Paratype articulated hindlimb skeleton of *Balearica exigua* new species, UNSM 53580.

Skull and Mandible. Paratype skull UNSM 53579: length of mandible, 71.3; greatest depth of mandible at surangular, 8.1; length of rostrum from posterior margin of nostril to tip, 45.5; greatest length of nostril opening, 29.1; height of quadrate from squamosal articulation to tip of orbital process, 12.1; pterygoid length, 9.1. See Table 1 for additional comparative measurements.

Pelvis. Paratype UNSM 53580: width across antitrochanters, 30.9; width across anterior expansion of ilia, 24.6; length of right ilium, from antitrochanter to anterior extent, 65.8.

Coracoid. Measurements of four specimens given in the sequence UNSM 96738, 96743, 96744, 96745: length from head to internal distal angle, 48.5, 55.8, 49.3, 54.3; length of glenoid facet, 12.2, 14.1, 12.1, 14.5; width of sternal end, 21.0, 25.8, 20.1, 25.4.

Scapula and Furcula. No meaningful measurements were obtainable from the scapula, with the exception of one measurement of the width of proximal end for UNSM 53576, 16.6. The same was true for the furcula. One measurement of hypocleidium depth for UNSM 53580 was 7.8; for UNSM 52582, 7.2.

Sternum. Paratype UNSM 53580: distance from carinal apex to xiphium, 117.5; costal margin (estimated), 34.8; depth of sternal keel from carinal apex to manubrial spine, 40.8.

Humerus. Overall length, 148.6 (paratype UNSM 96734), 144.7 (UNSM 53599), 155.1 (UNSM 53582); length of deltoid crest, 49.8 (paratype UNSM 96734), 48.9 (UNSM 96746); width distal end, 25.0 (paratype UNSM 96747), 26.2 (UNSM 96747).

Ulna and Radius. Total length: ulna, 173.5; radius, 169.8 (both from UNSM 53580).

Carpometacarpus. Total length, 86.0 (paratype UNSM 96737); 77.4 (UNSM 53576), 82.7 (UNSM 53582), 84.8 (UNSM 53905), 79.9 (UNSM 96748); maximum depth across metacarpals II and III, 10.6 (paratype USNM 96737), 11.1 (UNSM 96749), 12.8 (UNSM 53905).

Phalanges of Manus (Lengths). Digit II, total length, 20.1; digit III: phalanx 1, 34.0 (depth, 10.7), phalanx 2, 25.4; digit IV, 8.8 (all measurements from holotype UNSM 53576).

Femur. Total length, 80.2 (paratype UNSM 23579); width center of shaft, 6.9 (UNSM 23579), 7.8 (UNSM 96750); transverse diameter of head, 17.0 (UNSM 23579); width distal end, 17.2 (UNSM 23579), 19.7 (UNSM 96750).

Tibiotarsus. Total length, 144 (estimated from right and left elements from holotype UNSM 53576), 185 (estimate from several specimens); width through condyles, 14.8 (UNSM 96736); depth through condyles, 12.5 (UNSM 96736); width center of shaft, 7.4 (UNSM 96751), 6.9 (UNSM 96736). None of the preserved fibulae were suitable for measurement.

Tarsometatarsus. Total length, 117.4 (holotype UNSM 53576), 126.9 (paratype UNSM 53579), 131.6 (UNSM 53580), 125.2 (UNSM 53905); width across trochleae, 16.5 (paratype UNSM 53579); least width of shaft, 7.4 (UNSM 96753), 6.9 (UNSM 96736); proximal width, 16.5 (paratype UNSM 53579), 17.5 (UNSM 96752).

Phalanges of Pes (Lengths). Digit I, phalanx 1, 16.0 (UNSM 53905); digit II, phalanx 2, 23.9; phalanx 3, 14.7 (both from UNSM 53580); digit III, phalanx 1, 25.7; phalanx 2, 20.1; phalanx 3, 18.0; phalanx 4, 12.3 (all from paratype UNSM 53580); also in same order, 24.5, 17.8, 16.2, and phalanx 4 not available (from holotype UNSM 53576); digit IV, phalanx 1, 18.7; phalanx 2, 11.6; phalanx 3, 9.2; phalanx 4, 12.6; phalanx 5, 9.7 (all from paratype UNSM 53580).

DESCRIPTION. Figure 2 shows the only specimen (UNSM 53579) from which any morphological information could be gleaned. Compared to living *Balearica*, this fossil is decidedly smaller by approximately 20–25 percent. The inflated region of the frontal bones, characteristic of living *Balearica*, is clearly visible in the fossil. The anterior projection of this region is far beyond that of living *Balearica*, extending well beyond the nasal-frontal hinge, and it is less inflated. In fact, the anterior supraorbital region has a relatively much larger bony crest than in living *Balearica*. There may be some lateral compression from preservation, but it is clear that the anterior frontal region was relatively more developed than in living *Balearica*. The posterior region of the cranium where two lateral projections occur in

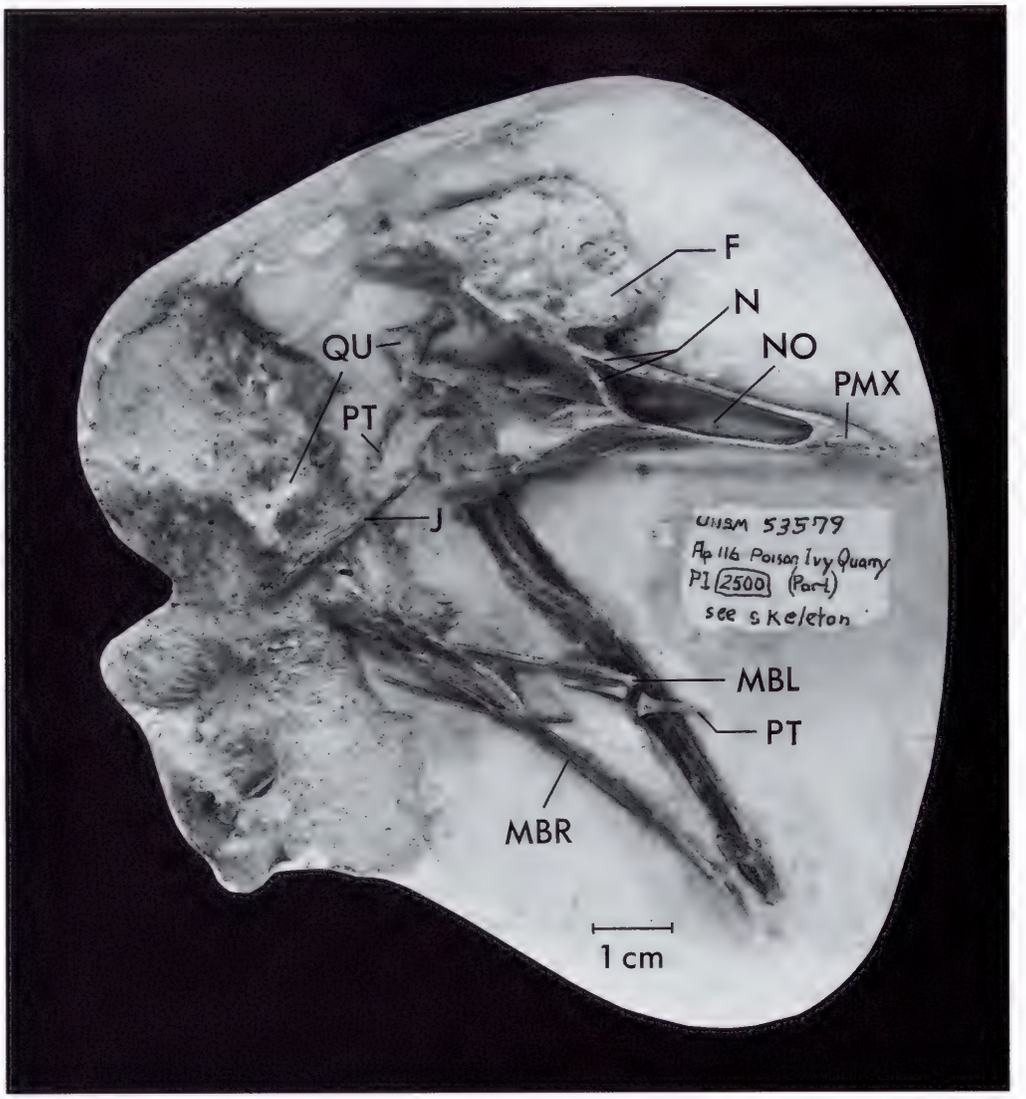

Figure 4. Paratype skull of *Balearica exigua* new species, UNSM 53579. Abbreviations: **F,** frontal; **J,** jugal; **MBL,** left mandible; **MBR,** right mandible; **N,** nasals; **NO,** narial opening; **PMX,** premaxilla; **PT,** pterygoid; **QU,** quadrate.

living *Balearica* is not preserved. The region of the rostrum is remarkably similar in the fossil and living *Balearica,* but the nasal opening excavates a more oval border anteriorly with the premaxilla. In the fossil the nasal struts are more angular in their contact with the frontals, and in ventral view the premaxillae are nearly parallel as they course posteriad, whereas in living *Balearica* the two bones diverge posteriad producing a more V-like appearance. The quadrate is virtually identical to that of living *Balearica.*

The fossil pelvis is very similar to that of living *Balearica,* except that the ilio-ischiatic fenestra is oval-shaped and less rounded. The distance between the posterior iliac crest and antitrochanter is relatively less and the posterior iliac crest has relatively less curvature.

The coracoid has the pneumatic fossa above the sternal facet less well developed than in living *Balearica,* and it is absent in smaller individuals of the fossil species. The sternal facet is less deeply grooved, and there is less of an internal distal angle at the sternal end. The procoracoid is less developed. The neck of the coracoid is not indented, and the coracohumeral surface is less produced. This brachial tuberosity has an overhanging rim with well-developed pneumatic foramina beneath in some individuals but absent in others. The scapulae are too poorly preserved for adequate comparison. The furcula is more robust than in living *Balearica,* with a prominent furcular process at the symphysis, in contrast to the near absence of a furcular facet in living *Balearica.* The symphysis forms a V-shaped point distally, not indented as in living *Balearica.* The furcula is more rounded at the symphysis and less flattened than in living *Balearica.*

The sternum is quite similar to that of living *Balearica,* but in living *Balearica* the dorsal aspect of the anterior carinal margin immediately ventral to the manubrial spine is pierced by one or more foramina but solid in the fossil. The coracoidal sulcus is shallower and less attenuate laterally in the fossil.

The humerus is very similar to that of living *Balearica* in overall features and proportions, but with the brachial depression less well developed and the attachment for m. latissimus dorsi anterioris is much less developed. The bicipital crest exhibits less of an overhanging rim than in living *Balearica.* The

Figure 5. Paratype elements of *Balearica exigua* new species, from left to right: right humerus, in anconal and palmar views, UNSM 96734; proximal left tibiotarsus, in lateral and medial views, UNSM 96735; right tibiotarsus, distal end, in posterior and anterior views, and insert view of distal end, UNSM 96736; right tarsometatarsus, in posterior and anterior views, and insert view of distal end, UNSM 53579.

radius, ulna, carpometacarpus, and bones of the manus exhibit no significant differences from those of living *Balearica*, except for size.

The femur is very similar to that of living *Balearica*, but with the posterior intermuscular line much less developed and the rotular groove less deeply excavated in the fossil species.

Except for size differences, the tibiotarsus and tarsometarsus of the fossil are virtually identical morphologically to those of living *Balearica*. There are minor qualitative differences, but when one considers the tremendous amount of individual variation in living *Balearica* these differences may be insignificant. The tarsometatarsus of living *Balearica* shows a more expanded hypotarsus with a relatively larger tendinal canal. In living *Balearica*, the inner cnemial crest of the tibiotarsus is slightly more expansive and extends relatively more distad. The outer cnemial crest is more prominently hooked and relatively more massive, possibly features associated with the large size of the living species. Distally in living *Balearica* there is a relatively deeper anterior intercondylar fossa and the supratendinal bridge is a more substantial bony structure. The internal condyle is more deeply excavated and the internal ligamental prominence is more pronounced. In anterior view, living *Balearica* shows a deeper and more extensive anterior metatarsal groove than that in the fossil.

DISCUSSION

In these fossil specimens from Nebraska, we have irrefutable evidence for the occurrence of crowned cranes (genus *Balearica*) in the upper Miocene of North America. In fact, this find confirms and bolsters previous identifications of such cranes in the fossil record (Brodkorb, 1967). This discovery is particularly important in that the fossils were recovered from a death assemblage indicating a habitat with wet grasslands not unlike that

of modern central and east African savannas, which is the precise habitat of modern African Crowned Cranes.

The fossil fauna is from a period when the forested regions of continental North America were greatly diminished and savannas had become the predominant vegetation, particularly in the center of the continent (Webb, 1977). As the savannas developed, open country faunas rapidly expanded, producing a wide array of ungulates occupying a habitat similar to those of modern central and east Africa. Ten million years ago in Nebraska, the climate was considerably warmer than at present, and an ocean of grass provided habitat for dozens of species of grazers, including rhinos, horses, camels, and prongbucks. In the wooded areas, large gomphotheres, tapirs, three-horned deer, and browsing horses ranged. Within the grazing horses, high-crowned (hypsodont) dentition developed, corresponding to the development of the plant families Gramineae and Leguminosae (Stebbins, 1952, 1974). This particular volcanic death assemblage was at a time "... when the ungulate fauna had reached its apogee" (Voorhies and Thomasson, 1979:331). Grass anthoecia recovered from the *Teleoceras* specimens indicate a diet of the grasses of the genus *Berriochloa* Elias 1932, a very common late Tertiary grass from the region (Voorhies and Thomasson, 1979). Evidence from symmetrically ripple-marked bedding planes within the ash deposits and remains of aquatic turtles and diatoms indicate the presence of standing water. Recent Crowned Cranes are non-migratory birds of open country that prefer wet grasslands or marshy conditions. One partially articulated fossil specimen (UNSM 53905) has a small lizard (a component of the diet of modern *Balearica*) the size of modern *Anolis carolinensis* Voigt 1832 preserved in the approximate position of the crop.

Historically there has been general agreement that *Balearica* is a primitive genus within the Gruidae, and the genus is quite distinctive anatomically from the other members of the family (Johnsgard, 1983). In fact, Brodkorb (1967) used a separate subfamily, the Balearicinae, to separate these primitive cranes from the remainder of the family, the Gruinae, which appears somewhat later in geologic time and includes the genera *Grus* and *Baeopteryx* Wetmore 1960. Many early students of bird evolution considered the limpkins, genus *Aramus* (Vieillot 1816), to be intermediate between rails and cranes (Fürbringer, 1888; Shufeldt, 1915), often with *Balearica* as a primitive crane leading into the Gruidae. However, Beddard (1898) and Mitchell (1915) emphasized the strong similarities between *Aramus* and cranes, a view more recently supported by Olson (1985), who considers *Aramus* as a primitive member of the Gruidae. He cites the extensive comparisons of the myology of *Aramus* by Allen (1962), who showed its crane-like musculature and revealed more similarities of *Aramus* to *Balearica* than to either *Grus* or the Rallidae. Cracraft (1973:115) also questioned the intermediacy of *Aramus* between rails and cranes and stated that "The similarities of *Aramus* and the Gruidae are more apparent when comparison is made to a crane with a more primitive skeleton such as that of *Balearica*." Wood (1979) performed an extensive computer-assisted phenetic comparison among living cranes. Treating *B. p. pavonina* and *B. p. regulorum* as separate species, his analyses showed, as expected, the *Balearica* species to form the most stable cluster, and the *Balearica* species were divergent from all other groups in six of ten analyses. Virtually all studies, including two recent DNA studies (Ingold et al., 1989; Krajewski, 1989), conclude that cranes of the genus *Balearica* are distinctive and primitive within the family Gruidae.

The extensive fossil record of cranes has been most recently reviewed by Olson (1985), who states that he examined specimens of North American fossil cranes that he considered to belong to the genus *Balearica* ranging in age from the early Oligocene (Chadronian) to late Miocene (Clarendonian). One of those he examined was the putative limpkin *Aramornis longurio* Wetmore 1926 (lower Miocene of Nebraska), and another was *Probalearica crataegensis* Brodkorb 1963 (lower Miocene of Florida). The latter is probably referable to *Aramornis* Wetmore 1926. Olson states that *Aramornis* may, in fact, not be separable from the genus *Balearica*. I have examined the spec-

Figure 6. Paratype elements of *Balearica exigua* new species, from left to right, upper to lower: left carpometacarpus, in internal view, UNSM 96737; left coracoid, dorsal view, UNSM 96738; right digit three, phalanx one, internal view, UNSM 96739; right radius, proximal end, UNSM 96740; right ulna, proximal end, internal view, UNSM 96741; left femur, posterior view, UNSM 23579.

imens of *Aramornis lonqurio* and *Probalearica crataegensis* and concur with Olson that these are *Balearica*-like cranes. However, these fossil taxa, being represented by single elements, may be very difficult to interpret in the overall picture of crane evolution. Two *Balearica*-like cranes are known from the Old World. Kurochkin and Ganya (1972) and Kurochkin (1985) described *Probalearica moldavia* (upper Miocene, Moldavian SSR) and *Probalearica mongolica* (Pliocene, central Asia), respectively, but both are known only from the distal ends of tibiotarsi.

The genus *Balearica* (including *Probalearica*) would appear to represent the primitive cranes within the family Gruidae. It is not surprising to find them as fossils in the mid-Tertiary of North America in paleohabitats similar to that enjoyed by living *Balearica* in Africa today. In addition to confirming older reports of *Balearica*-like cranes from North America, these specimens show that crowned cranes have remained in essentially the same type habitat for approximately 10 million years.

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TWO NEW LATE BLANCAN AVIFAUNAS FROM FLORIDA AND THE EXTINCTION OF WETLAND BIRDS IN THE PLIO-PLEISTOCENE

Steven D. Emslie

ABSTRACT. Two new late Blancan localities in Florida, Macasphalt Shell Pit and the St. Petersburg Times Site, have produced the largest fossil avifaunas of this age from eastern North America. These faunas comprise over 40 taxa, including one new genus and two new species of duck described herein, and the earliest fossil occurrence of condor (cf. *Gymnogyps* sp.), pygmy goose (*Anabernicula gracilenta*), and hawk-eagle (*Spizaetus* sp.). In addition, at least 20 extant species are represented and provide the most substantive information to date on the structure of wetland avifaunas during the Late Pliocene in Florida. Based on paleoecologic and taphonomic data and the outstanding preservation of fossil material, the avifauna from Macasphalt Shell Pit probably represents a biocoenose from a fresh or brackish water marsh.

Comparison of these faunas with younger, i.e., early and late Pleistocene, faunas from Florida provides an extinction chronology of wetland birds from one geographic region. The chronology indicates that most of the extinctions (14 of 17 taxa, or 82 percent) occurred to congeners of extant species, suggesting that species richness was decreasing in coastal wetlands during the Plio-Pleistocene. I hypothesize that eustatic changes in sea level over the past 2.5 million years caused extinction and extirpation of wetland birds through periodic inundation of coastal lowlands. This hypothesis can be tested with additions to the fossil record of Florida.

Key words: Blancan, Florida, avifaunas, wetlands, sea level changes, extinctions.

INTRODUCTION

The fossil record of birds from the upper Cenozoic of Florida is better known than that from any other geographic region of North America. However, Becker (1987), in summarizing the Neogene avifaunas of North America, listed only three Blancan localities from the eastern United States, all in Florida. These localities, Haile 15A in Alachua County, Santa Fe River 1B in Columbia County, and the St. Petersburg Times Site in Pinellas County, have produced only small collections of fossil birds.

Recent excavations at Macasphalt Shell Pit (currently APAC Shell Pit), Sarasota County (Fig. 1), have added a substantial collection of fossil birds, as well as other vertebrates, to the Blancan record of Florida. This locality first was known for its extraordinary invertebrate fauna (Petuch, 1982; Stanley, 1986; Lyons, 1991). Morgan and Ridgway (1987) discuss the vertebrate paleontology and mammalian biochronology of this site, whereas Lyons (1991) discusses the invertebrate biostratigraphy. Only the fossil equids among the vertebrates from this locality have been described in detail (Hulbert, 1988).

The avian collection from Macasphalt Shell Pit comprises over 400 bones of at least 40 species, including one new genus and two new species of duck described herein (Table 1). The avifauna from the St. Petersburg Times Site consists of 17 bones of 9 taxa (Table 1; for a preliminary list, see Becker, 1987). Both collections are dominated by species that currently inhabit coastal marshes and wetlands, indicating that a diverse avian community existed on the Gulf Coast of Florida in the Late Pliocene. These two fossil avifaunas are described here, and they are compared to other early and late Pleistocene avifaunas from Florida to establish an extinction chronology of wetland birds from one geographic region. This chronology is used to identify patterns in avian extinctions in the Plio-Pleistocene and to develop an hypothesis for the cause of these extinctions in coastal

Figure 1. Location of Blancan and Irvingtonian fossil localities in Florida.

Table 1. Fossil avifaunas of Macasphalt Shell Pit (MSP), St. Petersburg Times Site (SPTS), and Leisey Shell Pit (LSP; data from Emslie, in press), with total number of bones and minimum number of individuals in parentheses for each taxon. Extinct taxa are indicated by an asterisk (*).

Taxon	MSP	SPTS	LSP
**Gavia concinna*			3 (2)
Gavia immer			2 (1)
Podilymbus podiceps	99 (9)	7 (2)	27 (8)
Podiceps sp.			4 (2)
Pelecanus sp. cf. *P. erythrorhynchos*			3 (1)
Phalacrocorax sp.	3 (1)		8 (4)
Anhinga anhinga			2 (1)
Anhinga sp.			1 (1)
Botaurus lentiginosus	4 (2)		
**Botaurus* sp. (small)	2 (2)		
Ixobrychus exilis	1 (1)		
Ardea sp.	1 (1)		2 (1)
Casmerodius albus			3 (1)
Egretta sp. cf. *E. tricolor*			1 (1)
Egretta sp.	7 (2)		3
Nycticorax violaceus	2 (1)		
Eudocimus sp.	4 (1)	1 (1)	
**Eudocimus* sp. A (small)	3 (2)		1 (1)
**Ajaia* sp.			4 (2)
Plataleidae, indet.	2		1
**Ciconia maltha*	2 (1)		9 (2)
**Ciconia* sp.			1 (1)
**Teratornis* sp. cf. *T. incredibilis*			1 (1)
**Teratornis merriami*			8 (1)
**Gymnogyps kofordi*			6 (1)
**cf. Gymnogyps* sp.	1 (1)		1
Dendrocygna sp.	7 (2)		
Cygnus buccinator			5 (1)
Cygnus sp.			2
Branta canadensis	1 (1)		3 (1)
**Branta dickeyi*			3 (2)
Anserini, indet.	3		
**Anabernicula gracilenta*	3 (1)		4 (2)
**Helonetta brodkorbi* n. sp.	5 (2)		
Anas sp. cf. *A. crecca*	2 (1)		
Anas crecca			5 (3)
Anas discors		1 (1)	
Anas crecca or *A. discors*		2 (1)	13
Anas sp. cf. *A. cyanoptera*	25 (2)		
Anas platyrhynchos			2 (1)
Anas sp. cf. *A. clypeata*	6 (1)	1 (1)	
Anas sp. cf. *A. americana*	2 (1)		
Anas americana			1 (1)
Anas sp.			9
Aythya americana			6 (3)
Aythya marila			2 (1)
Aythya americana or *A. marila*			3
Aythya valisineria or *A. americana*	2 (1)		
Aythya collaris			2 (1)
Aythya affinis			9 (3)
Aythya collaris or *A. affinis*	6 (2)		9
Aythya sp.			8
Somateria sp. cf. *S. spectabilis*			1 (1)
cf. *Bucephala albeola*	3 (2)		6 (3)
Mergus serrator			1 (1)
Mergus merganser or *M. serrator*	3 (1)		
**Oxyura hulberti* n. sp.	5 (2)		
Anatidae, indet.	17		17
**Spizaetus* sp.	1 (1)		
Buteo sp.			1

Table 1. Continued.

Taxon	MSP	SPTS	LSP
Buteo sp. cf. *B. lineatus*			1 (1)
Aquila sp.			1 (1)
**Amplibuteo* sp.			6 (1)
Accipitridae, indet.			1
**Meleagris leopoldi/anza*	1 (1)		5 (2)
Colinus sp.			1 (1)
Laterallus sp.	8 (4)		
Rallus longirostris or *R. elegans*	4 (2)		1 (1)
Rallus limicola	69 (11)	1 (1)	
Rallus sp. cf. *R. limicola*	10 (2)		
**Rallus* sp. A	48 (9)	2 (1)	1 (1)
**Rallus* sp. B	13 (3)		
**Porphyrula* sp.	2 (1)	1 (1)	
Gallinula sp.	5 (1)		
Fulica americana			21 (5)
cf. *Fulica americana*	10 (2)	1 (1)	
Rallidae, indet.	5		
Grus canadensis	3 (1)		7 (2)
**Grus* sp. (large)			2 (2)
**Himantopus* sp.	2 (1)		
**Recurvirostra* sp.			2 (1)
Phoenicopterus ruber			2 (1)
**Phoenicopterus copei*			2 (1)
Phoenicopterus sp.	4 (1)		
**Phoenicopterus* sp. (small)	1 (1)		
cf. *Tringa* sp.	2 (2)		
Actitis macularia	11 (3)		
Limosa sp. cf. *L. fedoa*			1 (1)
Limnodromus sp.	4 (1)		
Gallinago sp.	1 (1)		
Scolopax sp.	1 (1)		
Scolopacidae, indet.	2		
Alcidae, indet.			2 (1)
Bubo virginianus			2 (1)
Corvus sp.			1 (1)
cf. *Agelaius phoeniceus*	11 (3)		
Icterinae, indet.	3		
Passeriformes, indet.	16		
Aves, indet.			18
Total	459 (95)	17 (10)	280 (80)

wetlands at the end of the Blancan, Irvingtonian, and Rancholabrean Land Mammal Ages.

MATERIALS AND METHODS

Recent and fossil skeletal collections were examined at the Florida Museum of Natural History, University of Florida (UF), and in the collections of Pierce Brodkorb (PB), Gainesville; the National Museum of Natural History, Smithsonian Institution (USNM), Washington, D.C.; the Natural History Museum of Los Angeles County (LACM), Los Angeles; the Museum of Vertebrate Zoology (UCMVZ), and the Museum of Paleontology (UCMP), University of California, Berkeley; and the Museum of Northern Arizona (MNA), Flagstaff. Measurements were taken with vernier calipers to the nearest 0.1 mm. All specimens from the St. Petersburg Times Site and Macasphalt Shell Pit are deposited in the vertebrate paleontology collections of the Florida Museum of Natural History (FLMNH).

SYSTEMATIC PALEONTOLOGY

Order Podicipediformes

Family Podicipedidae

Podilymbus Lesson 1831

Podilymbus podiceps (Linnaeus 1758)

REFERRED MATERIAL. St. Petersburg Times Site: 2 humeral ends right coracoids, UF 69726–69727; proximal right humerus, UF 69728; distal right humerus, UF 69729; distal right femur, UF 69730; proximal left tibiotarsus, UF 69731; distal right tibiotarsus, UF 69732.

Macasphalt Shell Pit: 3 maxillae, UF 94963, 95445, 95992; right squamosal, UF 95960; 2 left quadrates, UF 105763, 105775; right quadrate, UF 105762; proximal right mandible, UF 101410; 2 proximal left scapulae, UF 94673, 95760; 2 right scapulae, UF

95441, 105736; proximal right scapula, UF 105755; 3 left coracoids, UF 95433, 101407, 105737; 2 humeral ends left coracoids, UF 94964, 101437; right coracoid, UF 94978; humeral end right coracoid, UF 105838; 2 manubria of sterna, UF 94977, 95993; left humerus missing distal end, UF 93012; 4 proximal left humeri, UF 94953, 94969, 95439, 105835; 3 distal left humeri, UF 94967, 95438, 101441; 3 distal right humeri, UF 105738, 105836–105837; 2 proximal right radii, UF 95961, 105761; distal left radius, UF 100036; distal left ulna, UF 105847; distal right ulna, UF 94980; proximal right carpometacarpus, UF 94979; 3 left femora, UF 94954, 101406, 105739; distal left femur, UF 95431; 2 right femora, UF 94971, 94981; distal right femur, UF 94955; proximal left femur, UF 105743; 4 proximal left tibiotarsi, UF 94968, 94972, 95963, 95996; 8 distal left tibiotarsi, UF 94957–94958, 94973, 101403, 105730–105731, 105839–105840; 4 proximal right tibiotarsi, UF 94982, 95443, 105841–105842; 2 shafts right tibiotarsi, UF 94959, 94983; 5 distal right tibiotarsi, UF 94956, 95432, 100073, 105732–105733; left tarsometatarsus missing proximal end, UF 94965; 9 proximal left tarsometatarsi, 94960, 94966, 95434, 95436–95437, 95442, 100039, 100548, 105846; 5 distal left tarsometatarsi, UF 94976, 95435, 95440, 95444, 101436; 6 right tarsometatarsi, UF 94970, 94974–94975, 95942, 105740, 105843; 2 proximal right tarsometatarsi, UF 105734, 105741; 6 distal right tarsometatarsi, UF 94961–94962, 105735, 105742, 105844–105845.

DESCRIPTION. These specimens are identical in size and characters to the living species except for the maxillae, which are generally smaller and more slender (Table 2). Fossil species of grebes include *Podilymbus majusculus* Murray 1967 from Hagerman, Idaho, distinguished only by its larger size from *P. podiceps*, and *P. wetmorei* Storer 1976 from the upper Pleistocene of Florida, which is relatively more robust than *P. podiceps*.

DISCUSSION. *Podilymbus podiceps* was reported from Haile 15A, Alachua County, Florida (Campbell, 1976), and tentatively recognized from the Early Pliocene Bone Valley local fauna, Polk County, Florida (Becker, 1987). It appears to be a long-lived species that has experienced little change in morphology since the Late Pliocene.

Order Pelecaniformes

Family Phalacrocoracidae

Phalacrocorax sp.

REFERRED MATERIAL. Macasphalt Shell Pit: partial left quadrate, UF 94841; atlas vertebra, UF 95759; sternal end of left coracoid, UF 94679.

Order Ciconiiformes

Family Ardeidae

Botaurus Stephens 1819

Botaurus lentiginosus (Rackett 1813)

REFERRED MATERIAL. Macasphalt Shell Pit: humeral ends of 2 left coracoids, UF 94646–94647; sternal end right coracoid, UF 94831; manubrium of sternum, UF 94645.

DESCRIPTION. All specimens are similar to *Botaurus lentiginosus* in size (n = 4 females, UCMVZ), and the observed variation of osteological characters is within that seen in the modern species.

Botaurus sp.

REFERRED MATERIAL. Macasphalt Shell Pit: right coracoid, UF 105784; humeral end right coracoid, UF 101409.

DESCRIPTION. These specimens are distinctly smaller than *Botaurus lentiginosus* (n = 4 females, UCMVZ), *B. stellaris* (Linnaeus 1758) (n = 1 male, USNM), and *B. poiciloptilus* (Wagler 1827) (n = 1 female, USNM). Specimens of *B. pinnatus* (Wagler 1829) were not available, but this species is as large as *B. lentiginosus*.

Botaurus hibbardi Mosely and Feduccia 1975 was described on the basis of a distal femur from the Late Pliocene Rexroad local fauna, Kansas. No other elements are known for this extinct species, which also measures distinctly smaller than *B. lentiginosus*. It is possible that UF 101409 and 105784 represent this species.

MEASUREMENTS (mm). UF 101409: humeral breadth and depth, 6.4 and 7.9. UF 105784: length, 44.2; humeral breadth and depth, 6.7 and 7.5; least breadth and depth shaft, 3.2 and 2.5; sternal breadth, 11.6.

Ixobrychus Billberg 1828

Ixobrychus exilis (Gmelin 1789)

REFERRED MATERIAL. Macasphalt Shell Pit: proximal right humerus, UF 94911.

Ardea Linnaeus 1758

Ardea sp.

REFERRED MATERIAL. Macasphalt Shell Pit: humeral end left coracoid, UF 94833.

DESCRIPTION. This specimen is slightly smaller than females of *Ardea herodias* Linnaeus 1758 (n = 4, UCMVP) and equal in size to *A. cocoi* Linnaeus 1766 (n = 1, LACM). Characters of the humeral coracoid are variable in herons, particularly the relative size and morphology of the furcular facet and coracohumeral surface. Consequently, this specimen cannot be identified to species until additional comparative material is available.

Egretta Forster 1817

Egretta sp.

REFERRED MATERIAL. Macasphalt Shell Pit: 2 partial maxillae, UF 94834, 95946; humeral ends of 2 right coracoids, UF 94830, 94832; distal left tibiotarsus, UF 94694; proximal right tarsometatarsus, UF 105783; distal right tarsometatarsus, UF 113420.

DESCRIPTION. These specimens are too fragmentary for specific identification, but they are similar in size and characters to *Egretta thula* (Molina 1782), *E. tricolor* (Müller 1776), and *E. caerulea* (Linnaeus 1758).

Nycticorax Forster 1817

Nycticorax violaceus (Linnaeus 1758)

REFERRED MATERIAL. Macasphalt Shell Pit: distal left humerus, UF 94836; distal right tibiotarsus, UF 94835.

Table 2. Measurements (mm) of maxillae of *Podilymbus podiceps* compared to fossil specimens from Macasphalt Shell Pit. Abbreviations: LAN, length from anterior end of nares; DAN, depth at anterior nares; BAN, breadth at anterior nares; LBNB, least breadth nasal bar.

Specimen	LAN	DAN	BAN	LBNB
Females (n = 6)				
Range	9.3–10.9	3.8–4.8	3.9–4.7	1.8–2.2
Mean ± s.d.	9.9 ± 0.6	4.3 ± 0.4	4.3 ± 0.4	1.9 ± 0.2
Males (n = 5)				
Range	10.0–12.2	4.4–5.2	4.2–4.8	1.8–2.4
Mean ± s.d.	11.3 ± 0.8	4.8 ± 0.3	4.6 ± 0.3	2.1 ± 0.2
Fossil				
UF 94963	8.2	3.7	4.3	1.5
UF 95445	9.8	4.3	—	—
UF 95992	9.0	4.4	4.3	—

Family Plataleidae

Eudocimus Wagler 1832

Eudocimus sp.

REFERRED MATERIAL. St. Petersburg Times Site: shaft left coracoid, UF 69725.

Macasphalt Shell Pit: humeral end right coracoid, UF 113421; proximal left carpometacarpus, UF 94839; proximal right femur, UF 94838; proximal left tarsometatarsus, UF 113422.

DESCRIPTION. All specimens are from an ibis similar in size and characters to *Eudocimus albus* (Linnaeus 1758) or *E. ruber* (Linnaeus 1758).

Eudocimus sp. A

REFERRED MATERIAL. Macasphalt Shell Pit: distal left tibiotarsus, UF 113424; proximal left tarsometatarsus, UF 94644; proximal right tarsometatarsus, UF 100545.

DESCRIPTION. These specimens are from a small, extinct species of ibis described by Emslie (in press) from the late early Irvingtonian of Florida. This is the second record of this new taxon, which extends its geologic range into the Blancan.

Plataleidae, gen. et sp. indet.

REFERRED MATERIAL. Macasphalt Shell Pit: manubrium of sterum, UF 94643; fragment of distal right humerus, UF 100081.

DESCRIPTION. These specimens are too fragmentary for positive identification, but they are from a small ibis, probably *Plegadis* Kaup 1829 or *Eudocimus*.

Family Ciconiidae

Ciconia maltha L. Miller 1910

REFERRED MATERIAL. Macasphalt Shell Pit: partial right scapula, UF 100030; distal right radius, UF 100032.

DISCUSSION. This taxon was widespread in North America and has been reported from fossil localities of Blancan through Rancholabrean age (Brodkorb, 1963a; Feduccia, 1967). Other Blancan localities from which it has been identified include Hagerman and Snake River, Idaho (Feduccia, 1967; Miller, 1944), which are approximately 1 Ma older than the deposits at Macasphalt Shell Pit. Becker (1987) lists several Late Miocene records of *Ciconia* sp., including those from the late Clarendonian Love Bone Bed, Alachua County, Florida, and at least two species from the late Hemphillian Bone Valley local fauna of Florida and one species from Wickieup, Arizona.

Family Vulturidae

cf. *Gymnogyps* Lesson 1842

REFERRED MATERIAL. Macasphalt Shell Pit: proximal pedal phalanx, UF 113400.

DESCRIPTION. This specimen was compared to *Vultur gryphus* Linnaeus 1758 (n = 1), *Gymnogyps californianus* (Shaw 1798) (n = 5), *Sarcoramphus papa* (Linnaeus 1758) (n = 3), and *Teratornis merriami* L. Miller 1909 (n = 1). The proximal end in proximal view is deeper than it is wide in *V. gryphus* and *T. merriami*, wider than it is deep in *S. papa*, and as deep as it is wide in *G. californianus* and UF 113400. In addition, the fossil specimen compares well with the pedal phalanx (UF 69389) of *G. kofordi* Emslie 1988 from the late early Irvingtonian of Florida.

DISCUSSION. Prior to now, the earliest record of this genus was a proximal tibiotarsus from the very early Irvingtonian Inglis 1A locality, Citrus County, Florida (Speaker Carr, 1981). The extension of this genus into the Blancan provides additional support to the hypothesis that condors probably evolved in North America (Emslie, 1988).

Order Anseriformes

Family Anatidae

Subfamily Dendrocygninae

Dendrocygna Swainson 1837

Dendrocygna sp.

REFERRED MATERIAL. Macasphalt Shell Pit: humeral end left coracoid, UF 113437; right scapula, UF 105785; proximal left humerus, UF 113433; proximal right humerus, UF 113425; distal left humerus, UF 95981 (Fig. 2A); right carpometacarpus, UF 94845 (Fig. 2B); left femur, UF 117337; right tibiotarsus, UF 94801 (Fig. 2C).

DESCRIPTION. These specimens were compared to *Dendrocygna arborea* (Linnaeus 1758) (n = 2), *D. autumnalis* (Linnaeus 1758) (n = 6), *D. bicolor* (Vieillot 1816) (n = 5), *D. guttata*

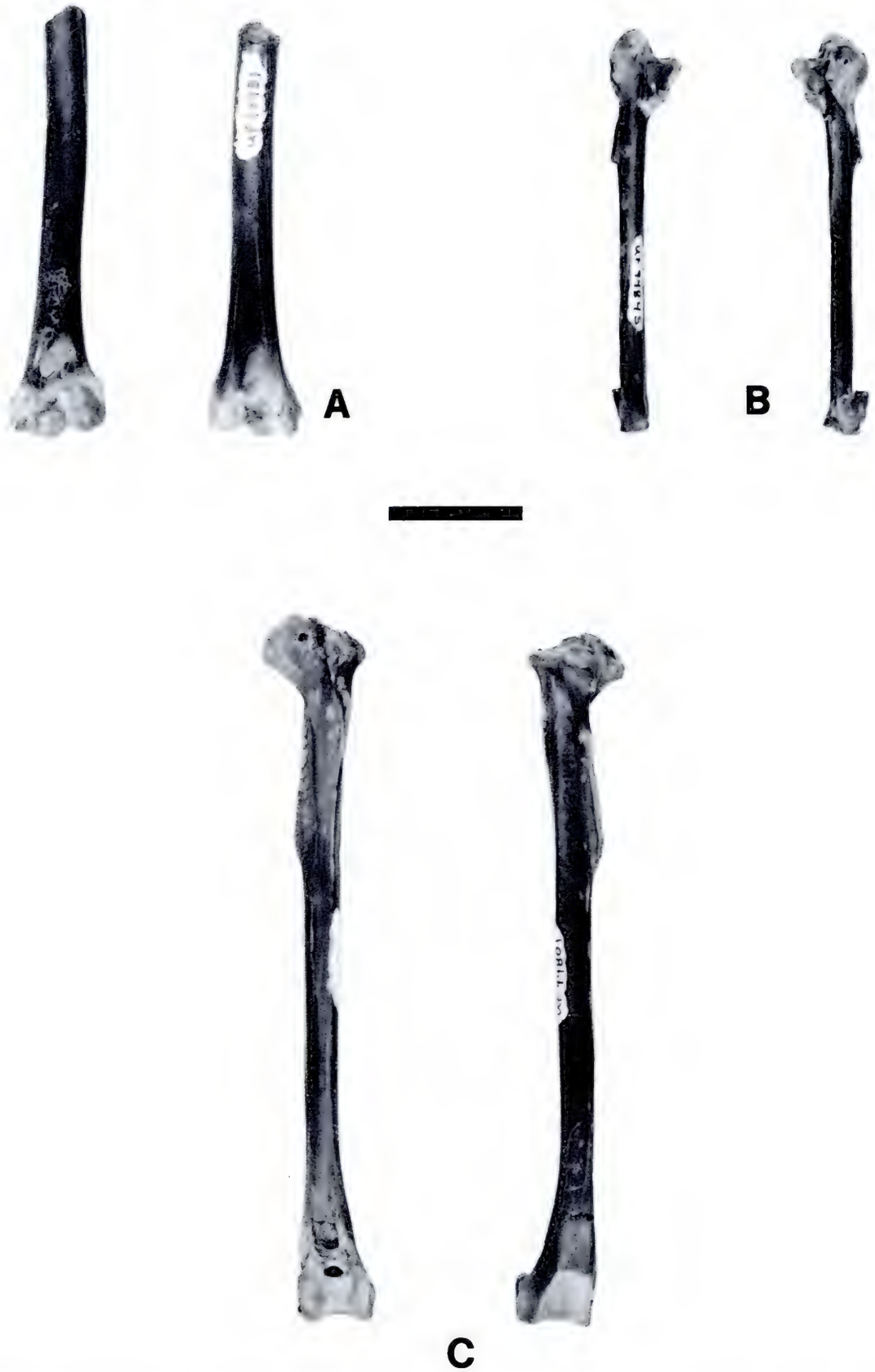

Figure 2. Specimens of *Dendrocygna* sp. from Macasphalt Shell Pit, Florida. **A,** Distal left humerus, UF 95981, in palmar (left) and anconal (right) views; **B,** right carpometacarpus, UF 94845, in external (left) and internal (right) views; **C,** right tibiotarsus, UF 94801, in anterior (left) and posterior (right) views. Scale 1×; scale bar = 2 cm.

Schlegel 1866 (n = 2), *D. viduata* (Linnaeus 1766) (n = 2), *D. eytoni* (Eyton 1838) (n = 2), *D. arcuata* (Horsfield 1824) (n = 2), and *D. javanica* (Horsfield 1821) (n = 2). Considerable variation in size and osteological characters was noted in the living taxa, precluding a specific identification of these specimens. The fossil specimens are generally larger and more robust than most Recent species. Only *D. arborea* has elements of comparable size and characters, except to UF 94801, which is shorter and more robust.

A small tree duck, *Dendrocygna eversa* Wetmore 1924 is known from the Late Pliocene (Blancan) Benson local fauna, Arizona. It was approximately half the size of living species and is known only by a proximal humerus (USNM 10547) that has a proximal breadth and depth measuring 14.9 and 5.2 mm, respectively. Compared to UF 113433 and 113425, USNM 10547 has a less pronounced head, a deltoid crest less flared, and a pectoral attachment extending lower on shaft. A large tree duck, *D. validipinnis* DeVis 1888, from the Pleistocene of Australia was described on the basis of a proximal humerus and ulna. It was shown by Olson (1977a) to be synonymous with *Biziura lobata* (Shaw 1796). An unidentified species also is known from the upper Miocene of Florida (Becker, 1985b).

MEASUREMENTS (mm). Humeri: UF 113433, proximal breadth and depth, 21.7 and 7.5; UF 113425, proximal depth, 8.0; UF 95981, least breadth and depth of shaft, 7.0 and 5.5, distal breadth and depth, 14.5 and 8.6. Carpometacarpus: UF 94845, length, 63.2, proximal breadth and depth, 6.1 and 12.0, least breadth and depth of shaft, 4.5 and 3.5, distal breadth and depth, 6.5 and 6.8. Tibiotarsus: UF 94801, length, 105.7, proximal breadth, 11.3, least breadth and depth of shaft, 5.5 and 4.3, distal breadth and depth, 11.7 and 12.2.

Subfamily Anserinae

Tribe Anserini

Branta canadensis (Linnaeus 1758)

REFERRED MATERIAL. Macasphalt Shell Pit: proximal left radius, UF 94605.

Anserini, gen. et sp. indet.

REFERRED MATERIAL. Macasphalt Shell Pit: 2 proximal left scapulae, UF 105848–105849; manubrium of sternum, UF 105850.

DESCRIPTION. These specimens are from a goose similar in size and characters to *Branta canadensis,* but they lack sufficient diagnostic features for generic identification.

Subfamily Tadorninae

Tribe Tadornini

Anabernicula Ross 1935

Anabernicula gracilenta Ross 1935

REFERRED MATERIAL. Macasphalt Shell Pit: distal right humerus, UF 113355; distal left carpometacarpus, UF 100038; distal left tarsometatarsus, UF 113366.

DESCRIPTION. These specimens compare well in size and characters with 5 humeri, carpometacarpi, and tarsometatarsi of this species from the McKittrick Tar Seeps, Kern County, California, at LACM. Four other species and one genus of extinct pygmy geese are known from North America. *Brantadorna downsi* Howard 1963 is known by a fragmentary proximal humerus and humeral coracoid from the lower Pleistocene of California and differs generically from *Anabernicula,* as discussed by Howard (1963). *Anabernicula minuscula* (Wetmore 1924) is a poorly known taxon from the Upper Pliocene of Arizona, and no comparable material from Macasphalt is available. *Anabernicula robustus* Short 1970 is known by a complete humerus from the lower Pleistocene of Nebraska; it is slightly larger and more robust than other *Anabernicula. Anabernicula oregonensis* Howard 1964 from the upper Pleistocene of Oregon differs from *A. gracilenta* in the distal humerus by having the attachment of anterior articular ligament more rounded with the facet facing more palmad. The humerus from Macasphalt Shell Pit agrees with *A. gracilenta* in these characters. Diagnoses of the distal carpometacarpus and tarsometatarsus were not provided by Howard (1964), but UF 100038 and 113366 are referred to *A. gracilenta* because of their close similarity in size and morphology to the specimens from the McKittrick Tar Seeps.

DISCUSSION. This is the third record for *Anabernicula gracilenta* in Florida and it extends the known range of this species into the Blancan. This species also is known from the very early Irvingtonian Inglis 1A local fauna (Speaker Carr, 1981) and Leisey Shell Pit 1A (Emslie, in press).

Subfamily Anatinae

Tribe "Anatini" *incertae sedis*

Helonetta new genus

TYPE SPECIES. *Helonetta brodkorbi* new species.

DIAGNOSIS. Humerus similar to that found in members of the tribe "Anatini" *incertae sedis* (see Livezey, 1986), and different from all other tribes of Anatinae, by characters given by Woolfenden (1961), including rim of pneumatic fossa circular and reduced, fossa lacking internal bony struts and shaft robust. Differs from that of *Nettapus* Brandt 1836 and *Chenonetta* Brandt 1836 in having proximal end not inflected, deltoid crest less flared, and pneumatic fossa less reduced and partly visible when viewed from internal side. Differs from that of *Aix* Boie 1828, *Pteronetta* Salvadori 1895, and *Cairina* Fleming 1822 in having relatively larger pneumatic fossa, less robust internal tuberosity, and bicipital crest angled more abruptly from shaft. Differs from that of *Anas* Linnaeus 1758, *Callonetta* Delacour 1936, and *Amazonetta* Boetticher 1929 in having a distinct expansion of attachment area between the proximal head and pectoral attachment in anconal view.

ETYMOLOGY. From Greek *helos,* neuter, for marsh, in reference to the habitat represented at Macasphalt Shell Pit, and *netta,* feminine, for duck.

Helonetta brodkorbi new species

Figure 3

HOLOTYPE. Complete right humerus, UF 93011 (Fig. 3B).

PARATYPES. Macasphalt Shell Pit: proximal left humerus, UF 113352; proximal right humerus, UF 94821 (Fig. 3A); distal right humerus, UF 94820 (Fig. 3A).

DIAGNOSIS. As for genus.

TYPE LOCALITY AND HORIZON. Macasphalt Shell Pit, Sarasota County, Florida. The holotype is from Unit 4 of Petuch (1982), Pinecrest Member of Tamiami Formation, Upper Plio-

Table 3. Measurements (mm) of humeri of *Nettapus coramandelianus* (n = 9; 3 males, 4 females, 2 unsexed) compared to fossil specimens of *Helonetta brodkorbi* n. gen. et sp. from Macasphalt Shell Pit. Abbreviations: L, total length; PB, proximal breadth; PD, proximal depth; LBS, least breadth shaft; LDS, least depth shaft; DB, distal breadth; DD, distal depth.

Specimen	L	PB	PD	LBS	LDS	DB	DD
Nettapus coramandelianus							
Range	53.6–57.9	11.1–12.3	3.9–4.8	3.6–4.3	3.2–3.6	7.8–8.8	5.3–5.7
x ± s.d.	56.2 ± 1.3	11.9 ± 0.4	4.4 ± 0.3	3.9 ± 0.2	5.4 ± 0.1	8.4 ± 0.3	5.0 ± 0.2
Helonetta brodkorbi							
UF 93011	66.1	14.2	5.0	4.4	3.7	9.3	5.6
UF 94820	—	—	—	5.2	4.3	9.8	6.5
UF 94821	—	14.0	4.8	—	—	—	—
UF 113352	—	14.3	5.5	—	—	—	—

cene; S½, NW¼, NE¼, Sec. 12, T36S, R18E; Bee Ridge Quadrangle.

MEASUREMENTS. See Table 3.

DESCRIPTION. The humeri of *Helonetta brodkorbi* compare most closely with those of *Nettapus* spp., tribe "Anatini," except that they are generally larger (Table 3) with a relatively narrower impression of m. brachialis anticus and a deeper olecranal fossa. The fossils are similar to humeri of *Nettapus* spp. in having a distinct expansion of attachment area between the proximal head and pectoral attachment in anconal view (Fig. 3). This character is partially developed in the tribe Tadornini and partially to well developed in *Nettapus* spp.

ETYMOLOGY. Named in honor of Pierce Brodkorb in recognition of his contributions to the study of Plio-Pleistocene avifaunas of North America.

DISCUSSION. Osteological comparisons of the fossil specimens with representative species from all tribes of Anatinae indicate that they are affiliated with the "Anatini" *incertae sedis* (Livezey 1986). This provisional tribe comprises "a poorly resolved grade of 'perching' and 'dabbling' genera" (Livezey, 1986: 743; including *Pteronetta, Cairina, Aix, Nettapus,* and *Anas*) that formerly were placed in the polyphyletic tribes "Anatini" and "Cairinini." Livezey has shown that these tribes lack derived characters that distinguish them from other anatid tribes, but he has maintained these genera in an unresolved phylogenetic group, "Anatini," until additional studies are completed. As *Helonetta* appears most closely related to *Nettapus,* it also is included in this group.

Species of *Nettapus* occur in freshwater ponds and marshes in Australia, Southeast Asia, and Africa (Johnsgard, 1978). The paleoecological conditions at Macasphalt Shell Pit (see later) indicate that *Helonetta brodkorbi* may have had ecological requirements similar to those of living pygmy geese. If *H. brodkorbi* is indeed related to living pygmy geese (not to be confused with pygmy geese of the tribe Tadornini; see earlier), it represents the first occurrence of this group in the New World.

Anas Linnaeus 1758

Anas sp. cf. *A. crecca* Linnaeus 1758

REFERRED MATERIAL. Macasphalt Shell Pit: humeral end right coracoid, UF 95995; proximal right carpometacarpus, UF 94964.

Anas discors Linnaeus 1766

REFERRED MATERIAL. St. Petersburg Times Site: left humerus, UF 69740.

Anas crecca or *A. discors*

REFERRED MATERIAL. St. Petersburg Times Site: left coracoid, UF 69739; right coracoid, UF 69738.

Anas sp. cf. *A. cyanoptera* Vieillot 1816

REFERRED MATERIAL. Macasphalt Shell Pit: left coracoid, UF 105765; right coracoid, UF 94828; sternal end right coracoid, UF 94814; proximal left scapula, UF 94826; proximal right scapula, UF 100035; proximal left humerus, UF 94824; 2 distal left humeri, UF 94808, 94817; right humerus, UF 101415; proximal right humerus, UF 94816; distal right humerus, UF 94829; proximal left ulna, UF 94823; 2 proximal right ulnae, UF 95624, 95994; distal left ulna, UF 95447; 2 distal right ulnae, UF 95623, 113361; proximal left radius, UF 105769; distal left radius, UF 95448; proximal right radius, UF 94822; left carpometacarpus, UF 113362; distal right carpometacarpus, UF 113364; distal left femur, UF 94811; distal right tibiotarsus, UF 100074; distal left tarsometatarsus, UF 105774.

DESCRIPTION. These specimens are tentatively referred to this species. They are similar in morphology to the living species, but they are slightly more robust.

DISCUSSION. *Anas cyanoptera* occurs today primarily in western North America and is rare in Florida (Sprunt, 1954). The specimens from Macasphalt Shell Pit, if indeed of that species, suggest it was common in Florida in the Late Pliocene.

Anas sp. cf. *A. clypeata* Linnaeus 1758

REFERRED MATERIAL. St. Petersburg Times Site: right carpometacarpus, UF 69741.

Macasphalt Shell Pit: left coracoid, UF 94606; distal left humerus, UF 113353, distal left ulna, UF 95958; distal right radius, UF 105770; distal left carpometacarpus, UF 94805; proximal right tarsometatarsus, UF 113368.

Figure 3. Right humeri of *Helonetta brodkorbi* n. gen. et sp., from Macasphalt Shell Pit, Florida. **A,** Anconal view of paratype proximal end, UF 94821, and paratype distal end, UF 94820 (do not make contact but probably are the same specimen); **B,** anconal (left) and palmar (right) views of UF 93011 (holotype). Scale 1×; scale bar = 1 cm.

Anas sp. cf. *A. americana* Gmelin 1789

REFERRED MATERIAL. Macasphalt Shell Pit: right coracoid, UF 94818; right tarsometatarsus lacking proximal end, UF 95635.

Tribe Aythyini

Aythya Boie 1822

Aythya valisineria (Wilson 1814) or *A. americana* (Eyton 1838)

REFERRED MATERIAL. Macasphalt Shell Pit: proximal left scapula, UF 101414; distal right carpometacarpus, UF 105768.

Aythya collaris (Donovan 1809) or *A. affinis* (Eyton 1838)

REFERRED MATERIAL. Macasphalt Shell Pit: humeral end right coracoid, UF 95980; proximal left scapula, UF 95762; proximal right scapula, UF 94825; distal right humerus, UF 113356; right carpometacarpus, UF 94827; proximal right carpometacarpus, UF 94804.

Tribe Mergini

Bucephala sp. cf. *B. albeola* (Linnaeus 1758)

REFERRED MATERIAL. Macasphalt Shell Pit: 2 distal right humeri, UF 95449, 113357; proximal right ulna, UF 113360.

DESCRIPTION. The distal humeri compare well in size and characters to this species except for the attachment of the internal articular ligament, which is less reflected away from the shaft in UF 95449 and 113357 than in the modern species.

DISCUSSION. Two fossil species of *Bucephala* are known. *Bucephala fossilis* Howard 1963 was described from a proximal carpometacarpus from the Vallecito Creek local fauna of the middle Pleistocene (Irvingtonian) of California. It is also known by a proximal humerus, proximal ulna, proximal scapula, and manubrium of a sternum. No diagnostic characters of the ulna, the only element shared with the material from Macasphalt,

Figure 4. Holotype left humerus, UF 95446, of *Oxyura hulberti* n. sp., in anconal (left) and palmar (right) views from Macasphalt Shell Pit, Florida. Scale 1×; scale bar = 1 cm.

were given by Howard. *Bucephala ossivallis* Brodkorb 1955 was based on a proximal coracoid from the Bone Valley Formation, Lower Pliocene (late Hemphillian) of Florida. It is larger than *B. albeola*, shares characters with *B. clangula* (Linnaeus 1758), and is not known by other elements.

Mergus Linnaeus 1758

Mergus merganser Linnaeus 1758 or *M. serrator* Linnaeus 1758

REFERRED MATERIAL. Macasphalt Shell Pit: proximal right scapula, UF 105773; distal right radius, UF 94810; proximal right humerus, UF 94815.

Tribe Oxyurini

Oxyura Bonaparte 1828

Oxyura hulberti new species

Figure 4

HOLOTYPE. Complete left humerus, UF 95446.

DIAGNOSIS. The holotype is referable to *Oxyura* by osteological characters given by Woolfenden (1961), including humerus with deep and broadly excavated surface of external head, slender shaft, slight elevation of facet for anterior articular ligament, and presence of ridge extending from external condyle to brachial depression.

The holotype differs from other species of *Oxyura* by having the deltoid crest in palmar view relatively shorter, with a more pronounced midpoint of crest, than that found in *O. jamaicensis* (Gmelin 1789) and *O. vittata* (Philippi 1860), and relatively larger and more robust than that of *O. dominica* (Linnaeus 1766); absence of deep excavation at attachment of m. internal triceps that is present in *O. vittata* and *O. maccoa* (Eyton 1838); attachment of anterior articular ligament expanded farther proximad on shaft than that of *O. jamaicensis* and *O. dominica* and larger than that of *O. vittata*, and impression of m. brachialis anticus relatively larger than that of *O. jamaicensis* and distinctly deeper than that of *O. dominica*.

TYPE LOCALITY. Macasphalt Shell Pit, Sarasota County, Florida. The specimen is from Unit 4 of Petuch (1982), Pinecrest Member of Tamiami Formation, Upper Pliocene; S½, NW¼, NE¼, Sec. 12, T36S, R18E, Bee Ridge Quadrangle.

MEASUREMENTS. See Table 4.

REFERRED MATERIAL. Left scapula, UF 94803; furculum, UF 94809; proximal left carpometacarpus, UF 94802; proximal right carpometacarpus, UF 105834.

DESCRIPTION. The humerus is relatively shorter but more robust in the shaft than in *Oxyura jamaicensis* (n = 7 females, 6 males, UCMVZ); *O. australis* Gould 1836 is larger and more robust than *O. jamaicensis* (n = 2, UCMVZ). *Oxyura maccoa* (n = 2, USNM) is much larger, and *O. dominica* is smaller (n = 2 females, 3 males, USNM). Only *O. vittata* (n = 1, USNM) approaches the size and proportions of the fossil species (Table 4). The carpometacarpus has a less robust metacarpal I and steeper angle where it merges with metacarpal II, and ligamental attachment of pisiform process relatively larger and blunter, than that of *O. jamaicensis*. *Oxyura dominica* has a less robust metacarpal I and an external ligamental attachment that only partially divides the carpal trochlea from metacarpal I; this groove completely divides the carpal trochlea from metacarpal I in UF 94802 and 105834. The scapula (UF 94803 and 94812) and furculum (UF 94809) lack diagnostic characters that distinguish them from *O. jamaicensis*.

Howard (1963) described *Oxyura bessomi* from a carpometacarpus (LACM 2785) from the middle Irvingtonian Vallecito Creek locality, California. This specimen differs from UF 94802 and 105834 by having a relatively longer and larger metacarpal I. Moreover, the posterior contour of the external crest does not recede as abruptly, and the posterior rim of the internal crest is not as deflected medially, in the specimens from Macasphalt Shell Pit. *Oxyura bessomi* also is known by a distal ulna and two coracoids, but these elements are unknown for *O. hulberti*.

Alvarez (1977) described *Oxyura zapatanima* from the Upper Pliocene/lower Pleistocene of Chapala, Mexico, from a nearly complete tibiotarsus. The specimen is smaller and more slender than tibiotarsi of *O. jamaicensis*. Alvarez also tentatively referred a distal worn humerus to this species based only on its association with the type tibiotarsus and admits that it is too worn to provide even familial characters. No tibiotarsi of *O. hulberti* are known, but, based on Alvarez's description of *O. zapatanima*, it is unlikely that these taxa are the same species.

ETYMOLOGY. Named for Richard C. Hulbert, Jr., who discovered the holotype, in recognition of his contributions to vertebrate paleontology in Florida.

DISCUSSION. Only one other species of *Oxyura* is known from deposits older than those that produced *O. hulberti*, and that is only a tentative identification of *O. dominica* from the Bone Valley Formation (Becker, 1987). *Oxyura hulberti* appears to be closely related to the living *O. jamaicensis*.

Anatidae sp. indet.

REFERRED MATERIAL. Macasphalt Shell Pit: 5 humeral ends left coracoids, UF 95622, 101431, 105766–105767, 113351; sternal end left coracoid, UF 94813; shaft right coracoid, UF 94819; distal left humerus, UF 113354; distal left ulna, UF 105793; 3 proximal left radii, UF 100031, 113358–113359; proximal right radius, UF 105771; 2 proximal right carpometacarpi, UF 94806–94807; distal left tarsometatarsus, UF 100079; distal right tarsometatarsus, UF 95979.

DESCRIPTION. UF 101431, 105766–105767, 113351, 94813, 113354, 100031, 113358–113359, 94807, 100079, and 95979 are from a small, teal-sized duck; UF 95622, 94819, 105771, and 94806 are from a duck equal in size to *Anas clypeata* or *Aythya affinis*. The specimens are too fragmentary for positive identification.

Order Accipitriformes

Family Accipitridae

Spizaetus Gray 1841

Spizaetus sp.

REFERRED MATERIAL. Macasphalt Shell Pit: distal left tibiotarsus, UF 113419.

DESCRIPTION. This specimen was compared to species of *Accipiter* Brisson 1760, *Buteo* Lacépède 1799, *Buteogallus* Lesson 1830, *Aquila* Brisson 1760, *Spizaetus* Vieillot 1816, *Spizastur* Gray 1841, *Amplibuteo* Campbell 1979, *Wetmoregyps* L. Miller 1928, *Neophrontops* L. Miller 1916, and *Neogyps* L. Miller 1916. The fossil specimen has a relatively deep intercondylar groove, and the morphology of the tendinal opening and bridge is similar to that in *Spizaetus* (n = 4, *S. ornatus* Friedmann

Table 4. Measurements (mm) of the humerus and carpometacarpus of *Oxyura jamaicensis, O. dominica,* and *O. vittata* (humerus only) compared to *O. hulberti* n. sp. Abbreviations as for Table 3.

Specimen	L	PB	PD	LBS	LDS	DB	DD
Humerus							
O. jamaicensis							
Females (n = 7)							
Range	68.0–69.3	14.4–15.4	5.1–5.4	3.6–3.9	3.4–3.7	8.3–8.8	5.5–6.3
x ± s.d.	68.6 ± 0.5	14.7 ± 0.4	5.3 ± 0.1	3.8 ± 0.1	3.5 ± 0.1	8.6 ± 0.2	6.0 ± 0.3
Males (n = 6)							
Range	68.9–72.6	14.3–15.0	5.1–5.6	3.6–3.8	3.5–3.8	8.5–8.7	5.9–6.5
x ± s.d.	70.6 ± 1.4	14.7 ± 0.3	5.4 ± 0.2	3.7 ± 0.1	3.6 ± 0.1	8.6 ± 0.1	6.2 ± 0.2
O. dominica							
n	3	5	5	3	3	4	4
Range	59.7–62.7	12.7–13.6	3.9–4.8	3.4–3.8	3.0–3.4	8.2–8.3	4.6–5.0
x ± s.d.	61.6 ± 1.7	13.3 ± 0.4	4.4 ± 0.4	3.7 ± 0.2	3.2 ± 0.2	8.3 ± 0.1	4.9 ± 0.2
O. vittata (n = 1, male)							
USNM 227491	68.2	14.7	4.8	3.6	3.4	8.4	5.3
O. hulberti n. sp.							
UF 95446	64.6	14.7	5.6	3.8	3.6	8.9	6.3
Carpometacarpus							
O. jamaicensis							
Females (n = 7)							
Range		3.5–3.8	7.5–7.8				
x ± s.d.		3.6 ± 0.1	7.6 ± 0.1				
Males (n = 6)							
Range		3.4–3.7	7.5–7.9				
x ± s.d.		3.6 ± 0.1	7.7 ± 0.1				
O. dominica (n = 4)							
Range		3.3–3.6	6.8–7.3				
x ± s.d.		3.5 ± 0.1	7.0 ± 0.2				
O. hulberti n. sp.							
UF 94802		3.6	7.5				
UF 105834		—	7.5				

1935); other genera examined, except *Aquila,* have a shallow intercotylar groove and differ from this fossil in the morphology of the tendinal opening and bridge. The tibiotarsus compares well with the fossil species *S. grinnelli* (L. Miller 1911), but it is much smaller in size (range of distal breadth in *S. grinnelli,* 18.6–19.6 mm; distal depth, 12.8–13.3 mm; n = 8, LACM). It may represent a new species, but it is too fragmentary for detailed systematic analysis.

MEASUREMENTS (mm). UF 113419: distal breadth, 15.1; depth at external condyle, 9.8.

DISCUSSION. Four fossil species of *Spizaetus* are known: *S. pliogryps* (Shufeldt 1891) from the upper Pleistocene of Fossil Lake, Oregon, *S. willetti* Howard 1935 from the upper Pleistocene of Nevada, *S. grinnelli* from the upper Pleistocene of California and Mexico (Brodkorb, 1964a), and *S. tanneri* Martin 1971 from the lower Pleistocene of Nebraska. Of these species, only *S. grinnelli* is known by the tibiotarsus.

Becker (1985c) tentatively referred one bone to *Spizaetus grinnelli* from the lower Pleistocene West Palm Beach fauna, Palm Beach County, Florida. His record was the first for this genus in the eastern United States. The specimen from Macasphalt is the second record, and it extends the geologic range of the genus into the Blancan. Two Recent species, *S. ornatus* and *S. tyrannus* Friedmann 1950, occur in tropical regions of Mexico and Central and South America, while eight other species occur in Southeast Asia and Africa (Clements, 1978).

Order Galliformes

Family Phasianidae

Meleagris Linnaeus 1758

Melagris sp.

REFERRED MATERIAL. Macasphalt Shell Pit: radiale, UF 94681.

DESCRIPTION. This specimen compares well with fossils of *Meleagris leopoldi* A.H. Miller and Bowman 1956/*M. anza* (Howard 1963) from the early Irvingtonian Inglis 1A fauna

Table 5. Comparative measurements (mm) of Recent and fossil humeri of *Laterallus* spp. Abbreviations as for Table 3.

Specimen	L	PB	PD	LBS	LDS	DB	DD
L. albigularis (n = 3, unsexed)							
Range	25.1–26.1	4.7–5.1	1.4	1.4	1.3–1.5	3.6–3.7	2.1–2.3
x ± s.d.	25.8 ± 0.5	4.9 ± 0.2	1.4 ± 0	1.4 ± 0	1.4 ± 0.1	3.6 ± 0.1	2.2 ± 0.1
L. jamaicensis (n = 4, 1 female, 3 males)							
Range	23.4–27.1	4.1–5.3	1.1–1.4	1.1–1.5	1.1–1.4	3.0–3.6	1.9–2.3
x ± s.d.	25.9 ± 1.7	4.9 ± 0.5	1.3 ± 0.1	1.4 ± 0.2	1.3 ± 0.1	3.4 ± 0.3	2.1 ± 0.2
L. ruber (n = 3, 1 female, 2 males)							
Range	25.7–27.5	5.4–5.5	1.4–1.5	1.5–1.7	1.4–1.6	3.8–4.0	2.2–2.4
x ± s.d.	26.8 ± 1.0	5.5 ± 0.1	1.5 ± 0.1	1.6 ± 0.1	1.5 ± 0.1	3.9 ± 0.1	2.3 ± 0.1
L. exilis (n = 2, males)							
USNM 511025	23.8	4.7	1.3	1.4	1.3	3.2	1.9
USNM 492233	23.7	4.6	1.3	1.3	1.2	3.3	1.9
L. leucopyrrhus (n = 3, 2 females, 1 unsexed)							
Range	26.0–29.1	5.0–5.4	1.3–1.4	1.5–1.8	1.3–1.6	3.6–3.9	2.1–2.3
x ± s.d.	26.2 ± 2.8	5.2 ± 0.2	1.4 ± 0.1	1.6 ± 0.2	1.4 ± 0.2	3.8 ± 0.2	2.2 ± 0.1
L. melanophaius (n = 3, 1 female, 1 male, 1 unsexed)							
Range	26.0–26.4	5.0–5.3	1.3–1.5	1.3–1.5	1.3	3.6–3.8	2.0–2.2
x ± s.d.	26.2 ± 0.2	5.1 ± 0.2	1.4 ± 0.1	1.4 ± 0.1	1.3 ± 0	3.7 ± 0.1	2.1 ± 0.1
L. viridis (n = 4, 1 female, 2 males, 1 unsexed)							
Range	27.5–28.4	5.7–6.2	1.5–1.8	1.8–2.0	1.6–1.9	4.3–4.8	2.3–2.7
x ± s.d.	28.1 ± 0.4	6.0 ± 0.2	1.7 ± 0.1	1.9 ± 0.1	1.8 ± 0.1	4.6 ± 0.2	2.6 ± 0.2
Laterallus sp. (fossil)							
UF 101401	25.7	4.4	—	1.5	1.4	3.7	2.2
UF 94844	—	—	—	1.7	1.5	3.9	2.2
UF 94843	—	—	—	—	—	3.4	2.0
UF 94842	—	—	—	—	—	3.7	2.2
UF 105758	—	—	—	—	—	3.7	2.3

(Steadman, 1980), but additional specimens are needed for specific identification.

Order Gruiformes

Family Rallidae

Laterallus Gray 1855

Laterallus sp.

REFERRED MATERIAL. Macasphalt Shell Pit: 4 distal left humeri, UF 94842–94844, 105758; right humerus, UF 101401; 2 right coracoids, UF 100033, 113375; right tarsometatarsus lacking proximal end and distal internal trochlea, UF 113417.

DESCRIPTION. The fossil humeri were compared to *Laterallus ruber* Sclater and Salvin 1860 (n = 3), *L. albigularis* (Lawrence 1861) (n = 4), *L. leucopyrrhus* Vieillot 1819 (n = 3), *L. melanophaius* Vieillot 1819 (n = 3), *L. exilis* Temminck 1831 (n = 3), *L. viridus* P.L.S. Muller 1776 (n = 4), and *L. jamaicensis* (Gmelin 1789) (n = 4) and found to differ from all of these species. Compared to the fossils, the impression of the m. brachialis anticus is relatively shallower and less distinct in *L. albigularis* and *L. jamaicensis* and narrower and deeper in *L. ruber* and *L. viridus*. The distal internal condyle is relatively larger in *L. leucopyrrhus*, *L. albigularis*, and *L. melanophaius* than in the fossils. The specimens are most similar to *L. exilis*, except for the generally smaller size of the latter (Table 5).

Two fossil species of *Laterallus* are known. Feduccia (1968) described *L. insignis* from the Late Pliocene Rexroad locality, Kansas, based on a distal right tibiotarsus. One other tibiotarsus was referred to this species, which is larger than *L. jamaicensis* and closest in characters to *L. leucopyrrhus* (Feduccia, 1968). Brodkorb (1952) described *L. guti* from the late Pleistocene Reddick locality, Florida. It is similar to *L. jamaicensis*, but more robust. Brodkorb (1967) later placed this species in the genus *Porzana* Vieillot 1816; however, Olson (1974) reexamined the holotype and, stating it could not be distinguished in size and most characters, synonymized it with the living *L. exilis*. Humeri from Macasphalt Shell Pit differ from *L. exilis* from Haile 11B, Florida (Olson, 1974), in having a broader distal end (Table 5).

Humeri from Macasphalt Shell Pit are larger and more robust than those of *Laterallus albigularis* and *L. jamaicensis* (Table 5) and may represent *L. insignis*, to which they cannot be compared. Other species of this genus were not at hand for comparison, necessitating the referral of these specimens to genus only until additional comparative material is available.

Rallus Linnaeus 1758

Rallus longirostris Boddaert 1783 or *R. elegans* Audubon 1834

REFERRED MATERIAL. Macasphalt Shell Pit: humeral end left coracoid, UF 95970; distal left tibiotarsus, UF 113396; 2 distal right tibiotarsi, UF 94670, 105751.

Table 6. Comparative measurements (mm) of Recent and fossil humeri of *Rallus* spp. Abbreviations as for Table 3.

Specimen	L	PB	PD	LBS	LDS	DB	DD
Recent species							
R. longirostris (n = 10, 6 females, 4 males)							
Range	50.7–56.6	8.6–10.5	2.6–3.4	2.8–3.4	2.3–2.8	6.6–8.0	3.9–4.5
x ± s.d.	53.9 ± 1.9	9.7 ± 0.6	3.0 ± 0.2	3.1 ± 0.2	2.6 ± 0.2	7.2 ± 0.4	4.2 ± 0.2
R. elegans (n = 9, 3 females, 5 males, 1 unsexed)							
Range	63.0–58.1	11.0–11.8	3.2–3.9	3.4–3.9	2.8–3.3	7.7–8.9	4.5–5.3
x ± s.d.	60.0 ± 1.8	11.4 ± 0.3	3.6 ± 0.2	3.6 ± 0.2	3.1 ± 0.2	8.4 ± 0.4	5.0 ± 0.3
R. limicola[1] (n = 10)							
Range	33.6–39.2	6.1–7.4	—	1.9–2.1	—	4.5–5.1	—
x	35.6	6.8	—	2.0	—	4.7	—
Fossil species							
R. prenticei[1] (n = 4)							
Range	36.1–41.0	7.1–8.0	—	2.1–2.6	—	5.1–5.4	—
x	39.1	7.6	—	2.4	—	5.3	—
Rallus sp. B							
UF 94919	44.0	8.9	2.5	2.8	2.4	6.1	3.5
UF 105744	—	8.1	2.4	—	—	—	—
UF 95758	—	9.0	2.6	—	—	—	—

[1] Measurements from Feduccia (1968).

DESCRIPTION. It is difficult to identify species within this genus by osteological characters of postcranial elements. Although it is possible to identify some species on the basis of their relative size, this is not the case with the largest North American rails, *Rallus longirostris* and *R. elegans*. As the fossil specimens are within the size range of both these species, they cannot be specifically identified.

Rallus limicola Vieillot 1819

REFERRED MATERIAL. St. Petersburg Times Site: proximal left tibiotarsus, UF 69735.

Macasphalt Shell Pit: left coracoid, UF 101408; 4 left coracoids lacking sternal end, UF 94926, 95988, 105759, 113372; sternal end left coracoid, UF 94940; 4 right coracoids, UF 94668, 94905–94907; humeral end right coracoid, UF 113376; 7 right coracoids lacking sternal end, UF 94657, 94928, 94933, 95977, 95990, 113373–113374; 3 proximal left scapulae, UF 94656, 105747, 113377; proximal right scapula, UF 113378; 3 proximal left humeri, UF 94693, 95966, 101438; distal left humerus, UF 113381; right humerus, UF 105760; 4 proximal right humeri, UF 94901, 95972, 105745, 113383; 3 distal right humeri, UF 94676, 95973, 113384; proximal left ulna, UF 113385; proximal right ulna, UF 94850; proximal right radius, UF 113379; 2 distal left carpometacarpi, UF 113390–113391; distal right carpometacarpus, UF 113393; proximal left femur, UF 113394; 3 proximal left tibiotarsi, UF 94654, 101405, 105833; 4 distal left tibiotarsi, UF 94655, 94902, 101435, 105756; 3 proximal right tibiotarsi, UF 113397–113399; 5 distal right tibiotarsi, UF 94658, 94920, 105749, 113401–113402; proximal left tarsometatarsus, UF 105748; 2 distal left tarsometatarsi, UF 94663, 101539; right tarsometatarsus, UF 95974; 4 proximal right tarsometatarsi, UF 94908, 94688, 113404, 113406; 5 distal right tarsometatarsi, UF 94672, 94848, 95976, 105746, 113412.

DESCRIPTION. These fossils compare well in size and proportions to modern specimens of this species.

Rallus sp. cf. *R. limicola*

REFERRED MATERIAL. Macasphalt Shell Pit: left coracoid, UF 94664; distal left ulna, UF 113386; left carpometacarpus, UF 94846; 2 proximal left tibiotarsi, UF 94660–94661; 2 distal left tibiotarsi, UF 94692, 94921; proximal right tibiotarsus, UF 95969; 2 distal right tibiotarsi, UF 94691, 105752.

DESCRIPTION. These specimens are slightly larger in size with a more robust shaft than *Rallus limicola*. They may represent the supposed subspecies *R. l. auffenbergi* (Brodkorb 1954), originally described as *Porzana auffenbergi*, but recognized as a slightly more robust form of *R. limicola* by Olson (1974). Additional study of this possible fossil subspecies is needed.

Rallus sp. A

REFERRED MATERIAL. St. Petersburg Times Site: distal right tibiotarsus, UF 69736; distal right tarsometatarsus, UF 69737.

Macasphalt Shell Pit: 2 left coracoids, UF 95944, 113371; 2 proximal right scapulae, UF 94924, 94929; left carpometacarpus, UF 113389; 2 proximal left carpometacarpi, UF 95634, 95989; distal left carpometacarpus, UF 105790; proximal left femur, UF 94925; distal left femur, UF 94913; proximal left tibiotarsus, UF 105754; 8 distal left tibiotarsi, UF 94914, 95954, 95967–95968, 95997, 101440, 105832, 113395; right tibiotarsus lacking distal end, UF 94903; proximal right tibiotarsus, UF 101412; 5 distal right tibiotarsi, UF 94659, 94904, 94915, 94935, 105753; 2 proximal left tarsometatarsi, UF 94667, 113405; 9 distal left tarsometatarsi, UF 94917–94918, 95975, 95998, 101411, 105750, 113407–113408, 113410; 4 proximal right tarsometatarsi, UF 94665, 94686, 94689, 94847; 7 distal right tarsometatarsi, UF 94662, 94687, 94690, 95953, 100075, 113415, 113418.

DESCRIPTION. These specimens are from a rail larger than *Rallus limicola* but distinctly smaller than *R. longirostris* and *R. elegans* (Tables 6, 7). They are only slightly larger in size than *R. prenticei* (Wetmore 1944) from Rexroad and Hagerman, discussed by Feduccia (1968), and they may represent that species.

MEASUREMENTS. See Tables 6 and 7.

Table 7. Comparative measurements (mm) of tibiotarsi of species of *Rallus*. Abbreviations as for Table 3.

Specimen	DB	DD
Rallus limicola[1] (n = 10)		
Range	3.8–4.6	4.0–4.9
x	4.2	4.4
R. prenticei[1] (n = 10)		
Range	4.5–5.1	4.8–5.5
x	4.8	5.1
R. longirostris (n = 6)		
Range	6.8–7.8	7.3–8.6
x ± s.d.	7.3 ± 0.4	7.9 ± 0.6
R. elegans (n = 10)		
Range	6.5–7.5	6.9–8.4
x ± s.d.	7.0 ± 0.3	7.7 ± 0.4
Rallus sp. A (n = 9)		
Range	4.8–5.2	4.8–5.5
x ± s.d.	5.1 ± 0.1	5.2 ± 0.2
Rallus sp. B		
UF 94666	5.5	5.9

[1] Measurements from Feduccia (1968).

Rallus sp. B

REFERRED MATERIAL. Macasphalt Shell Pit: left coracoid, UF 100546; right coracoid, UF 94912; left humerus, UF 94919; proximal left humerus, UF 95758; proximal right humerus, UF 105744; distal left tibiotarsus, UF 94666; 2 proximal left tarsometatarsi, UF 100037, 113403, 3 distal left tarsometatarsi, UF 94909–94910, 94916; proximal right tarsometatarsus, UF 94931; distal right tarsometatarsus, UF 95985.

DESCRIPTION. These specimens are slightly larger than *Rallus* sp. A and smaller than *R. longirostris* and *R. elegans*. The humeri and tibiotarsus are equal in size to *Pardirallus lacustris* (Brodkorb 1958) (Tables 6, 7), a species originally described as *Porzana lacustris* from the Upper Pliocene of Hagerman and Rexroad. Later, Feduccia (1968) transferred the species to the genus *Rallus* based on similarities to the Recent species *R. sanguinolentus* Swainson 1838. Olson (1973), however, has shown that *R. sanguinolentus, R. nigricans* Vieillot 1819, and *R. maculatus* Boddaert 1783 are not closely related to *Rallus* and should be placed in the genus *Pardirallus* Bonaparte 1856. He subsequently transferred *R. lacustris* to the genus *Pardirallus* (Olson, 1977b). Osteological characters that distinguish *Pardirallus* from *Rallus* include the presence of a deep pit in the anterior intercotylar fossa of the tibiotarsus, and tarsometatarsus with robust shaft. Neither of these characters are present in the material here. *Rallus phillipsi* Wetmore 1957, known by a complete tarsometatarsus from the Upper Pliocene of Arizona, was found by Olson (1977b) to be within the size range of *R. longirostris*.

MEASUREMENTS. See Tables 6 and 7.

DISCUSSION. The large number of *Rallus* bones from Macasphalt Shell Pit eventually may help determine the systematic position of many previously described rallid species in North America. It is clear that the systematic status of some fossil species is uncertain and in need of additional study. Until a detailed study can be completed, and as more fossil material is recovered from Macasphalt Shell Pit, these specimens can be referred to *Rallus* based on close similarities to that genus.

Porphyrula Blyth 1852

Porphyrula sp.

REFERRED MATERIAL. St. Petersburg Times Site: proximal left tarsometatarsus, UF 69733.

Macasphalt Shell Pit: proximal right tarsometatarsus, UF 94922; distal right tarsometatarsus, UF 113423.

DESCRIPTION. These specimens are similar to *Porphyrula martinica* (Linnaeus 1766) except in the distal tarsometatarsus (UF 113423), which has a relatively larger distal foramen and longer middle trochlea than in the living species (n = 1, UCMVZ). This material probably represents a new species of *Porphyrula*, but additional specimens are needed for adequate diagnosis.

Gallinula Brisson 1760

REFERRED MATERIAL. Macasphalt Shell Pit: sternal end right coracoid, UF 95987; proximal right humerus, UF 95945; distal right radius, UF 113380; proximal left carpometacarpus, UF 94932; proximal right carpometacarpus, UF 113392.

DESCRIPTION. These specimens are similar to *Gallinula chloropus* (Linnaeus 1758), except that the proximal humerus (UF 95945) has a more pointed head in palmar view and the sternal end of the coracoid (UF 95987) is less curved, in distal view, than in the living species.

Brodkorb (1967) described *Gallinula kansarum* from the Late Pliocene Rexroad locality, Kansas. Though it is known by other elements, diagnostic characters are given only for the distal humerus, and all other existing material is in need of additional study. McCoy (1963) described *G. brodkorbi* from the upper Pleistocene of Florida, but Olson (1974) reexamined the holotype and synonymized that species with *G. chloropus*, recognizing it as a large temporal subspecies, *G. c. brodkorbi*. Campbell (1980), however, recognized *G. brodkorbi* at the specific level. The Macasphalt Shell Pit specimens are too fragmentary for detailed comparison with fossil and living species.

Fulica sp. cf. *F. americana* Gmelin 1789

REFERRED MATERIAL. St. Petersburg Times Site: shaft left tarsometatarsus with distal internal trochlea, UF 69734.

Macasphalt Shell Pit: maxilla, UF 113369; left coracoid lacking sternal end, UF 113370; humeral end right coracoid, UF 94675; right coracoid lacking sternal end, UF 95986; manubrium of sternum, UF 94949; distal left humerus, UF 113382; distal right humerus, UF 105757; distal left ulna, UF 113387; proximal right tarsometatarsus, UF 113411; distal right tarsometatarsus, UF 94671.

DESCRIPTION. All specimens compare well with *Fulica americana* except for their generally smaller size, excluding UF 113369 and 94671, which are equal in size to the living species. Brodkorb (1961) described *Fulica infelix* from the Lower Pliocene Juntara Formation, Oregon, based on a distal tibiotarsus that is slightly smaller than *F. americana*. Unfortunately it is not known by other elements, making it impossible to compare with those from Macasphalt Shell Pit. Howard (1963) described *F. hesterna* from the Irvingtonian Vallecito Creek locality, California, but Olson (1974) synonymized this species with *F. americana*. *Fulica shufeldti* Brodkorb 1964, originally described as *F. minor* Shufeldt 1891, is recognized by its smaller size compared to *F. americana* (Brodkorb, 1964b). However, Howard (1946) found this species to overlap in size with the living species and considered *F. shufeldti* to be a temporal subspecies of *F. americana*, an opinion shared by Jefferson (1985). The new

material indicates that a small form of *Fulica*, perhaps a temporal subspecies of *F. americana*, was present during the Late Pliocene as well as the Pleistocene in North America.

Rallidae gen. et sp. indet.

REFERRED MATERIAL. Macasphalt Shell Pit: manubrium of sternum, UF 94930; left coracoid, UF 95971; distal left tibiotarsus, UF 100076; proximal right tibiotarsus, UF 94677; shaft right tarsometatarsus, UF 95951.

DESCRIPTION. UF 94930 is from an unidentifiable small rail, equal in size to *Rallus limicola*. All other specimens are from large rails near the size of *R. elegans*.

Family Gruidae

Grus canadensis (Linnaeus 1758)

REFERRED MATERIAL. Macasphalt Shell Pit: proximal right carpometacarpus, UF 102546; proximal left tarsometatarsus, UF 94603; distal left tarsometatarsus, UF 94604.

DESCRIPTION. The referred material compares well in size and characters to *Grus c. canadensis*.

Order Charadriiformes

Family Recurvirostridae

Himantopus Brisson 1760

Himantopus sp.

REFERRED MATERIAL. Macasphalt Shell Pit: distal left tibiotarsus, UF 101402; proximal right tarsometatarsus, UF 94948.

DESCRIPTION. The tibiotarsus (UF 101402) differs from *Himantopus mexicanus* (P.L.S. Müller 1776) in having a relatively larger tendinal opening and a distinct ridge connecting the prominence on the internal side of the internal condyle to the shaft (*H. mexicanus* has little or no ridge here). The tarsometatarsus (UF 94948) is larger with a deeper anterior metatarsal groove and smaller facet on the anterior-external border of the external cotyla than in *H. mexicanus*.

Bickart (1990) described *Himantopus olsoni* from the Early Pliocene Wickieup fauna, Arizona, based on a tarsometatarsus; numerous other skeletal elements were referred to this species as well. The tibiotarsus from Macasphalt Shell Pit is larger than those of the Wickieup species, and the tarsometatarsus (UF 94948) has a relatively less robust hypotarsus and less flared proximal shaft.

MEASUREMENTS (mm). Tibiotarsus: UF 101402, distal breadth and depth, 6.9 and 8.7, least breadth and depth of shaft, 3.3 and 3.0. Tarsometatarsus: UF 94948, proximal breadth and depth, 7.7 and 8.7.

DISCUSSION. This material probably represents a new species of stilt, but additional material is needed for adequate description.

Family Phoenicopteridae

Phoenicopterus Linnaeus 1758

Phoenicopterus sp.

REFERRED MATERIAL. Macasphalt Shell Pit: proximal left mandible, UF 94680; sternal end right coracoid, UF 94642; manubrium of sternum, UF 105782; distal left humerus, UF 94602; proximal left tarsometatarsus, UF 94601.

DESCRIPTION. All specimens compare well in size and characters to *Phoenicopterus ruber* Linnaeus 1758 except UF 94601, which is robust in the shaft but less broad at the proximal end, and UF 94602, which has an elongated attachment of anterior articular ligament compared to the living species (n = 3; also see measurements in Howard, 1946).

Four fossil species of *Phoenicopterus* have been described from North America: *P. floridanus* Brodkorb 1953 and *P. stocki* L. Miller 1944 from the Lower Pliocene (late Hemphillian) of Florida and Mexico and *P. copei* Shufeldt 1891 and *P. minutus* Howard 1955 from the Pleistocene of Oregon and California (Brodkorb, 1963a). Of these taxa, the first is known only by a proximal carpometacarpus, distal tibiotarsi, and distal tarsometatarsi (including additional material referred by Becker, 1985b), and it cannot be compared to the material here. *Phoenicopterus copei* is a large flamingo now known from the Irvingtonian of Florida (Emslie, in press) and the upper Pleistocene of California and Oregon (Howard, 1946, 1955; Jefferson, 1985). *Phoenicopterus minutus* and *P. stocki* are smaller than *P. ruber*, but the latter is known only by a distal tibiotarsus, and it cannot be compared to material here.

Proximal tarsometatarsi (LACM 2445 and 2473) of *Phoenicopterus minutus* from Manix Lake, California, were compared to UF 94601. These specimens are slightly smaller than UF 94601 (proximal breadth and depth, 14.2 and 16.0; 15.1 and 17.1 mm, respectively), the intercotylar prominence is less broad in *P. minutus*, and the cotylae are relatively broader and deeper in UF 94601. The shaft of LACM 2445 also is more slender (least breadth and depth, 5.7 and 6.5 mm) than that of UF 94601.

MEASUREMENTS (mm). Coracoid: UF 94602, sternal breadth and depth, 24.1 and 13.5. Tarsometatarsus: UF 94601, proximal breadth, 15.6, least breadth and depth of shaft, 6.6 and 7.7.

DISCUSSION. Two species of flamingo are possibly represented in the material from Macasphalt Shell Pit, one closely affiliated with the living species *Phoenicopterus ruber* and one smaller species that cannot be identified with the present material. However, a large size variation between sexes occurs in the living species (Becker, 1985b).

Family Scolopacidae

Tringa Linnaeus 1758

Tringa sp.

REFERRED MATERIAL. Macasphalt Shell Pit: 2 proximal left tarsometatarsi, UF 95991, 105764.

DESCRIPTION. These specimens compare well in size and characters to *Tringa melanoleuca* (Gmelin 1789) (n = 4, UCMVZ) except for a slightly broader shaft in the fossils. *Tringa flavipes* (Gmelin 1789), *T. solitaria* Wilson 1813, and *T. glareola* Linnaeus 1758 are distinctly smaller than *T. melanoleuca*; specimens of other living species of *Tringa* were not available for comparison.

Feduccia (1970) described *Tringa antiqua* from the Upper Pliocene of Kansas based on a complete humerus. This species differed from *T. solitaria* in its shorter and more robust size and in other osteological characters given by Feduccia. As the material from Macasphalt Shell Pit is larger than *T. solitaria*, it probably does not represent *T. antiqua*.

MEASUREMENTS (mm). UF 95991: proximal breadth and depth, 5.4 and 5.5, least breadth and depth of shaft, 2.4 and 1.9. UF 105764: proximal breadth and depth, 5.9 and 6.0.

Actitis macularia (Linnaeus 1766)

REFERRED MATERIAL. Macasphalt Shell Pit: 2 left coracoids, UF 94946, 95982; humeral end left coracoid, UF 94938; sternal end left coracoid, UF 94952; 2 right coracoids, UF 94648, 105780; 3 left humeri, UF 95943, 100550, 101413; right humerus, UF 95965–95966; proximal right humerus, UF 113429.

DESCRIPTION. These specimens fall within the size and range of variation of *Actitis macularia*. *Actitis hypoleucus* (Linnaeus 1758) (n = 1, UCMVZ) is larger and more robust than *A. macularia*. Becker (1985b) tentatively referred three bones to this genus from the Upper Miocene (late Clarendonian) of Florida; no other fossil records of this taxon are known.

Limnodromus Wied 1833

Limnodromus sp.

REFERRED MATERIAL. Macasphalt Shell Pit: left coracoid with damaged humeral end, UF 94941; proximal left humerus, UF 94683; distal left humerus, UF 94685; proximal left ulna, UF 113430.

DESCRIPTION. These specimens were compared to *Aphriza virgata* (Gmelin 1789) (n = 2, UCMVZ), *Arenaria* Brisson 1760, *Bartramia longicauda* (Bechstein 1812) (n = 2, UCMVZ), *Limnodromus scolopaceus* (Say 1823) (n = 2, UCMVZ), and *L. griseus* (Gmelin 1789) (n = 4, UCMVZ). The distal humerus (UF 94685) is distinguished from *Aphriza* Audubon 1839 by the ectepicondylar prominence, which protrudes from the shaft farther proximally and more abruptly in *Aphriza;* in addition, the coracoid (UF 94941) has a relatively larger scapular facet and narrower sternal facet. The distal humerus and coracoid of *Arenaria* cannot be distinguished from UF 94685 and 94941 but are distinctly larger in size than the fossil specimens. The distal humerus of *Bartramia* Lesson 1831 has a reduced ectepicondylar prominence and relatively smaller attachment of anterior articular ligament, and a coracoid with a broader sternal facet, compared to the fossil specimens. In *Limnodromus,* the ectepicondylar prominence also is reduced in *L. scolpaceus* but similar to UF 94685 in *L. griseus*. The fossil specimens compare most closely to *L. griseus,* except for a slightly larger size, and are therefore referred to this genus. Additional fossil material is needed to determine if these specimens represent a living or extinct species.

Gallinago Brisson 1760

Gallinago sp.

REFERRED MATERIAL. Macasphalt Shell Pit: distal left humerus, UF 94684.

DESCRIPTION. The fossil compares well to *Gallinago gallinago* (Linnaeus 1758) (n = 6, UCMVZ), particularly by the greatly reduced ectepicondylar prominence, but is much smaller in size (mean distal breadth of *G. gallinago,* 6.0 mm, range 5.7–6.2, n = 6). It may represent an extinct species but is too poorly known for adequate comparison and description.

MEASUREMENTS (mm). UF 94684: distal breadth, 5.4; least breadth and depth shaft, 2.5 and 2.2.

Scolopax Linnaeus 1758

Scolopax sp.

REFERRED MATERIAL. Macasphalt Shell Pit: left coracoid with damaged humeral end, UF 94942.

DESCRIPTION. This specimen compares well with the distinctive species *Scolopax minor* Gmelin 1789 (n = 4, UCMVZ), especially in the relative position of muscle scars. The fossil differs from this species in having a longer and more rectangular-shaped coracohumeral surface. *Scolopax rusticola* Linnaeus 1758 (n = 1, UCMVZ) is much larger in size.

Scolopacidae gen. et sp. indet.

REFERRED MATERIAL. Macasphalt Shell Pit: humeral end left coracoid, UF 101442; distal right tibiotarsus, UF 94937.

DESCRIPTION. The partial coracoid, UF 101442, is similar to *Tringa melanoleuca* except it has a narrower head. The distal tibiotarsus, UF 94937, compares well with *Limnodromus griseus* but is too fragmentary for positive identification.

Order Passeriformes

Family Emberizidae

Subfamily Icterinae

Agelaius Vieillot 1816

cf. *Agelaius phoeniceus* (Linnaeus 1766)

REFERRED MATERIAL. Macasphalt Shell Pit: 2 partial maxillae, UF 95627, 105779; distal mandible, UF 113444; 2 left humeri, UF 101404, 101416; left humerus lacking proximal end, UF 95763; right humerus, UF 95630; right coracoid, UF 94992; 2 distal right tibiotarsi, UF 94989, 105781; proximal left tarsometatarsus, UF 94987.

DESCRIPTION. These specimens were compared to *Dolichonyx* Swainson 1827, *Euphagus* Cassin 1867, *Molothrus* Swainson 1832, *Icterus* Brisson 1760, and *Agelaius* and *Xanthocephalus* Bonaparte 1850, and they are most similar to *Agelaius,* specifically *A. phoeniceus*. Given the amount of geographic variation that can occur within this species, the specimens are only tentatively assigned to this genus and species.

Icterinae gen. et sp. indet.

REFERRED MATERIAL. Macasphalt Shell Pit: partial right quadrate, UF 94991; proximal left mandible and symphysis, UF 95626; proximal right humerus, UF 95628.

DESCRIPTION. These specimens are too fragmentary for positive identification. All specimens, except UF 95626, appear to represent a blackbird similar to *Agelaius* sp. UF 95626 compares most closely to *Icterus;* however, no specimens of *Pandanaris* A.H. Miller 1947, an extinct genus known from Florida and California (Brodkorb, 1978), were available for comparison.

Passeriformes gen. et sp. indet.

REFERRED MATERIAL. Macasphalt Shell Pit: partial maxilla, UF 95941; proximal left mandible, UF 94990; proximal right mandible, UF 94652; proximal right humerus, UF 94994; distal right humerus, UF 105778; proximal right ulna, UF 94988; distal right ulna, UF 94939; 2 manubria of sternum, UF 94986, 94993; humeral end left coracoid, UF 95978; humeral end right coracoid, UF 100029; proximal right scapula, UF 94985; proximal right tibiotarsus, UF 94653; 3 distal right tarsometatarsi, UF 94995, 95631, 95983.

AGE AND COMPARISON TO OTHER BLANCAN AVIFAUNAS

The biostratigraphy, paleoecology, and vertebrate paleontology of the St. Petersburg Times Site and Macasphalt Shell Pit, as well as several other Blancan localities in Florida (Fig. 1), are reviewed and discussed by Morgan and Ridgway (1987). They show that numerous mammalian taxa from these localities are shared with Blancan faunas in western North America that have been dated using paleomagnetic and radiometric techniques. A late Blancan (2.0–2.5 Ma) age for the Florida faunas is indicated, especially by the co-occurrence of the South American taxa (*Glyptotherium* Osborn 1903, *Neochoerus* Hay 1926, *Dasypus* Linnaeus 1758, *Holmesina* Simpson 1930, and *Glossotherium* Owen 1840) that entered North America during the Great American Interchange and by North American taxa with restricted geologic ranges or associations with other taxa, such as *Nannippus peninsulatus* (Hay 1899) and *Trigonictis macrodon* (Cope 1868). This age is supported by the invertebrate biostratigraphy and geochemistry as well (Lyons, 1991; Jones et al., 1991). Moreover, the large number of extant taxa of birds from Macasphalt Shell Pit gives strong support for a Late Pliocene age for Unit 4 (Pinecrest Beds; Petuch, 1982), the bone-bearing layer at this site, when most living taxa of birds begin to appear in the fossil record. In contrast, the rich Pliocene avifaunas from Rexroad, Kansas, and Hagerman, Idaho, which date to the late Blancan (3.5 Ma) or approximately 1 Ma earlier than Macasphalt, are composed primarily of extinct taxa (Feduccia, 1975).

The addition of the St. Petersburg Times Site and Macasphalt Shell Pit faunas to the fossil record provides substantial information on vertebrate communities during what was once a poorly known time period in Florida that is approximately 2–3 Ma younger than the well-known Bone Valley local fauna (Brodkorb, 1955; Becker, 1987) and about 1 Ma older than the Irvingtonian faunas of Inglis 1A, Haile 16A, and Leisey Shell Pit (Emslie, 1988; Hulbert and Morgan, 1989).

Previously described Blancan avifaunas in Florida include Haile 15A, from which Campbell (1976) described a species of green heron (*Butorides validipes*) and reported Pied-billed Grebe (*Podilymbus podiceps*), Great Egret (*Casmerodius albus* Linnaeus 1758), Green-winged Teal (*Anas crecca*), Quail (*Colinus* sp. cf. *C. suilium* Brodkorb 1959), and Turkey (*Meleagris gallopavo* Linnaeus 1758) (for reinterpretation of this last species, see Steadman, 1980). Brodkorb (1963b) described *Titanis walleri*, a large phorusrhacoid, from bottom deposits in Santa Fe River 1B that have produced fossils of Eocene, Pliocene, and Pleistocene age (Morgan and Ridgway, 1987). Six other taxa, all extant, are known from this site, but the age of the specimens is unknown (Becker, 1987). Six other Blancan localities discussed by Morgan and Ridgway (1987) have produced no known remains of fossil birds.

PALEOECOLOGY AND TAPHONOMY

The paleoecology of Macasphalt Shell Pit as shown by the invertebrate fauna is discussed by Petuch (1982). He considered Unit 4, the primary bone-bearing unit at the site and the source for all specimens reported here, to represent a quiet, brackish water estuary, probably near the mouth of a river, based on the presence of potamidids and the black stain of the matrix resulting from an organic-rich environment. This interpretation is supported by a vertebrate fauna that is dominated by sirens (*Siren* sp.) and water snakes (*Nerodia* sp.), taxa restricted to freshwater habitats today, and freshwater and brackish water fish (Morgan and Ridgway, 1987).

The fossil avifauna also contributes to this paleoecological interpretation. The most abundant taxa, in number of bones and least number of individuals, are Pied-billed Grebe (*Podilymbus podiceps*) and collectively at least nine species of rails (five *Rallus* spp. and one each *Laterallus* sp., *Porphyrula* sp., *Gallinula* sp., and *Fulica* sp.) (Table 1). The Pied-billed Grebe is resident in Florida today on freshwater ponds and lakes throughout the state (Sprunt, 1954). Rails occur in fresh water and brackish water habitats throughout Florida, typically in areas with shallow ponds and marshes with abundant emergent vegetation. Other taxa from Macasphalt Shell Pit (herons, ibis, flamingo, shorebirds, ducks, blackbirds) are suggestive of marshes and exposed mud flats where wading birds can feed and of coastal estuaries where mollusks, a preferred food of some ducks and shorebirds, are available. These species are typical of tidal freshwater marshes where species diversity changes seasonally (Odum et al., 1984).

The taphonomy of the deposits at Macasphalt Shell Pit is complex. Avian remains from Unit 4 evidently occupy their primary site of deposition. A biocoenose is indicated by the high species richness and relative abundance of wetland birds, their outstanding preservation, including complete maxillae, skull fragments, and complete limb bones, and the rarity of strictly terrestrial or pelagic species (for additional discussion of the taphonomy, see Hulbert, 1988). Similar paleoecologic and taphonomic interpretations can be applied to the deposits at the St. Petersburg Times Site (Morgan and Ridgway, 1987).

Hulbert (1988) has indicated that the deposits in Unit 4 at Macasphalt Shell Pit must have formed when sea level was at or near its present level, and therefore either before or after the Late Pliocene glacial maximum at 2.4–2.5 Ma. As the age of the deposit has been established at 2.0–2.5 Ma, and after the earliest South American mammals reached Florida (Morgan and Ridgway, 1987), deposition must have occurred during a period of marine transgression. The maximum height obtained by this transgression is unknown, but mussel beds directly above and below Unit 4 indicate the presence of a shallow, offshore marine environment (Petuch, 1982).

DISCUSSION

The excellent samples of fossil birds from Macasphalt Shell Pit and the St. Petersburg Times Site are the largest of their age from eastern North America. The avifauna represented by these and other Blancan sites in Florida provide new information on the distribution of extant and extinct taxa, the latter of which include the earliest fossil occurrence of condor (cf. *Gymnogyps* sp.), pygmy goose (*Anabernicula gracilenta*), and hawk-eagle (*Spizaetus* sp.). In addition, these faunas are dominated by aquatic and wading species and can be compared to younger, or early and late Pleistocene, faunas from Florida to develop an extinction chronology of wetland birds for the Plio-Pleistocene.

The apparent time of origination and geologic range of all extinct, wetland taxa now known from Plio-Pleistocene localities in Florida were used to establish the chronology (Fig. 5). Lundelius et al. (1983) list 26 late Rancholabrean (25,000–10,000 B.P.) sites from which over 80 extant but only 3 extinct taxa are known. These faunas include Rock Springs in Orange County (Woolfenden, 1959), Itchtucknee River in Columbia County (McCoy, 1963; Campbell, 1980), Seminole Field in Pinellas County, Bradenton in Manatee County, Hog Creek and Venice Beach in Sarasota County, Vero in Indian River County, and Melbourne in Brevard County (Wetmore, 1931; Becker, 1985a). Not included in their summary are the large collections from

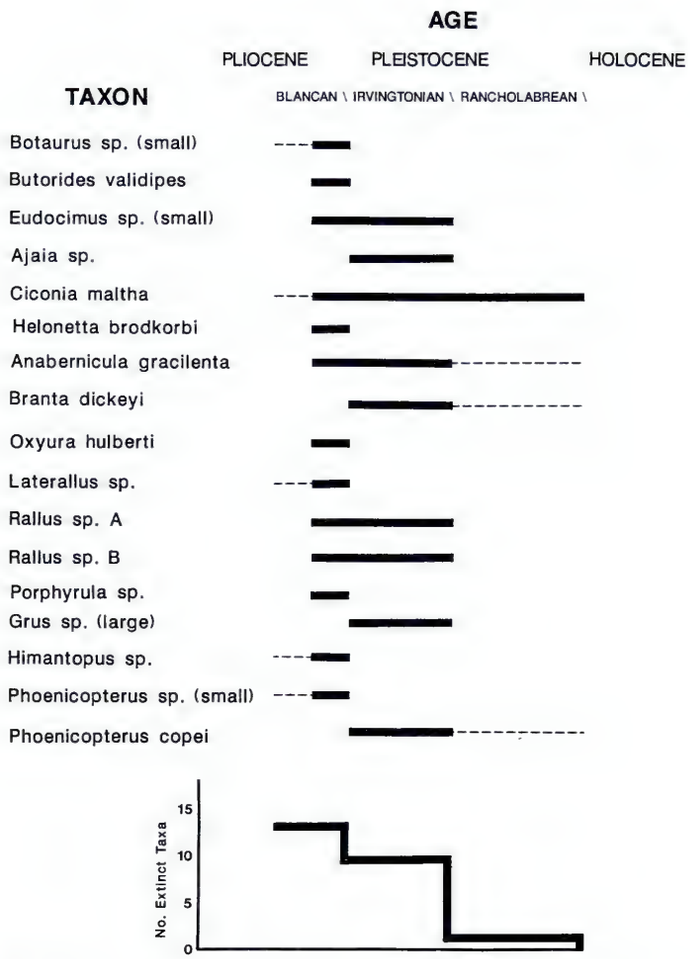

Figure 5. Extinction chronology of wetland birds in the Plio-Pleistocene of Florida. Solid lines indicate geologic ranges in Florida; dashed lines indicate ranges outside of Florida. Extinct taxa include undescribed species from Macasphalt Shell Pit and Leisey Shell Pit (see text for discussion of these taxa).

Reddick in Marion County and Arredondo in Alachua County, which date earlier than 25,000 B.P. (Brodkorb, 1957, 1959; Hamon, 1964). These faunas include over 60 taxa, including at least 9 extinct species.

Early Pleistocene faunas include those from Inglis 1A in Citrus County (47 taxa; Steadman, 1980; Speaker Carr, 1981), Coleman IIA, IIIC, and IIID in Sumter County (38 taxa; Ritchie, 1980), and Payne Creek in Polk County (10 taxa; Steadman, 1984). The most extensive Irvingtonian avifauna from Florida (exclusive of Inglis 1A) is that of Leisey Shell Pit in Hillsborough County (Table 1). It consists of over 40 primarily wetland taxa, including an extinct spoonbill (*Ajaia* sp.), a small ibis (*Eudocimus* sp.), known also from Macasphalt Shell Pit, and a condor (*Gymnogyps kofordi*) (Emslie, 1988, in press).

All of these faunas contribute to a remarkable record of wetland birds that spans the last 2.5 Ma and forms the basis for an extinction chronology for these birds. Obvious problems with this chronology are the vagaries of the fossil record. Taxa not known from one land-mammal age may simply not be preserved in younger or older deposits because of different taphonomic processes. It also is possible that some extant wetland taxa in Florida were locally extirpated in the past and recolonized at a later period. These events are invisible in the fossil record and preclude a precise estimate of species richness at any one time. The extinction chronology, however, is testable and subject to revision with additions to the fossil record.

PATTERNS IN AVIAN EXTINCTIONS

Figure 5 indicates that apparent extinctions or extirpations in Florida can be inferred for at least 17 taxa (including one new genus, two new species, and eight undescribed species). Eight taxa disappear in the Blancan, eight in the Irvingtonian (four of which originated during this time period) and one in the Rancholabrean. In addition, 14 of these extinctions (82 percent) occurred to congeners of extant species. (Species of the genera *Ciconia*, *Helonetta*, and *Anabernicula* are extinct in North America.)

Congeners that disappeared by the end of the Blancan include a heron (*Butorides validipes*), a small bittern (*Botaurus* sp.), and perhaps a small flamingo (*Phoenicopterus* sp.). Extinctions by the end of the Irvingtonian included a small ibis (*Eudocimus* sp. A), two species of rails (*Rallus* sp. A and B), and a large crane (*Grus* sp.). In addition, a large flamingo (*P. copei*), a large goose (*Branta dickeyi* L. Miller 1924), and one species of pygmy goose (*Anabernicula gracilenta*) so far are not known from deposits younger than the Irvingtonian in Florida but occur in Rancholabrean deposits in western North America (Emslie, in press; Fig. 5). These species apparently became locally extirpated but survived in the west until the end of the Pleistocene.

In addition to the above taxa, Leisey Shell Pit also has produced a single bone each of a small species of stork (*Ciconia* sp.), a small cormorant (*Phalacrocorax* sp.) and an anhinga (*Anhinga* sp.), and two bones of a large heron (*Ardea* sp.), that may represent extinct species (Emslie, in press). If so, this would increase the number of extinctions at the end of the Irvingtonian to 12, and the total number of extinctions to congeners of extant taxa to 17.

AN HYPOTHESIS FOR AVIAN EXTINCTIONS IN FLORIDA

The chronology indicates that fewer extinct taxa are present in progressively younger faunas, despite the originations that also occurred during this time. If this chronology represents real trends in fossil history, what would cause a decline in wetland species, especially congeners of extant species, through time? Webb (1974) and Webb and Wilkins (1984) discuss some of the probable effects of changing sea levels on Pleistocene mammalian faunas, when maximum and minimum sea levels nearly eliminated or doubled, respectively, the area of terrestrial habitat in Florida. I postulate that periodic fluctuations in sea level throughout the Plio-Pleistocene caused the loss of rich, coastal wetland habitat during interglacial periods, impacting avian communities. These habitats today are among the richest in the world and support a high species diversity of plants, invertebrates, birds, and mammals (Mitsch and Gosselink, 1986).

Direct evidence for the impact of sea-level changes on coastal lowlands in Florida is apparent at Macasphalt and Leisey Shell Pits, as well as numerous other localities. At these sites, over 2–3 m of shell beds that represent a shallow, offshore marine environment overlie the bone-bearing deposits (Petuch, 1982; Hulbert and Morgan, 1989). As many as eight other sea-level changes occurred after deposition of these faunas (1.2–0.9 Ma), with a possible maximum stand at 20–30 m above present sea

level (Cronin, 1980, citing van Donk, 1976; see also Opdyke et al., 1984, and Lyons, 1991). Moreover, Florida's low topography and peninsular geography would magnify the effects of only slight fluctuations in sea level and cause substantial loss of habitat that was not apparent in other regions with higher topography. Continued and frequent loss of habitat in a geologically brief period may have caused the extinction and extirpation of certain wetland species, especially those with restricted ecological requirements or a relatively large body size and low reproductive rate compared to their living congeners (see Pimm et al., 1988). If so, further systematic and morphologic studies of fossil birds from Florida may provide additional evidence for these extinction patterns.

SUMMARY AND CONCLUSIONS

Two new fossil avifaunas from the Upper Pliocene of Florida are the largest collections of this age from eastern North America. They add over 40 primarily wetland taxa (genera and species) to the fossil record and include at least 12 extinct and 20 extant species. These avifaunas also extend into the Blancan the geologic range of several genera (e.g., *Gymnogyps, Anabernicula, Spizaetus*), previously known only from younger faunas, and indicate that a diverse community of wetland birds once existed along the Gulf Coast of Florida.

The fossil avifauna from Macasphalt Shell Pit probably represents a biocoenose, based on paleoecologic and taphonomic data and the outstanding preservation of fossil material. The bone-bearing unit at this site is located between layers of marine shells and appears to have formed when sea level was at or near its present height. The avifauna and other vertebrates and invertebrates, and the black stain of the matrix caused by an organic rich environment, indicate that deposition occurred in a freshwater or brackish water marsh.

The addition of these avifaunas to the fossil record of Florida allows development of an extinction chronology of wetland birds from one geographic region that spans the last 2.5 Ma. At least 17 taxa, especially congeners of extant species, have apparently become extinct or extirpated in Florida since the Blancan. Assuming that most extant wetland birds in Florida survived and/or recovered from environmental changes during this period, the loss of congeners through time suggests that species richness was decreasing, despite the originations that also occurred during this time. It is possible that geologically frequent rises in sea level during interglacial stadials caused the loss of coastal habitat and the extinction and extirpation of certain taxa. This hypothesis is testable with additions to the fossil record.

Finally, Brodkorb (1966) suggested that all living species of birds did not appear until the Pleistocene, based on his studies of Pliocene faunas in Florida and western North America. The youngest Pliocene faunas cited by Brodkorb at that time were from Rexroad, Kansas, and Hagerman, Idaho, both of which date 1 Ma older than the faunas reported here (Lundelius et al., 1987). It now is apparent that many living species appeared by the Late Pliocene (see also Feduccia, 1968) and that the fossil populations often differed in size and relative limb proportions from Recent populations of the same species.

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QUATERNARY

BIRDS

THE AVIFAUNAS OF THE ISOLATED MEDITERRANEAN ISLANDS DURING THE MIDDLE AND LATE PLEISTOCENE

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ABSTRACT. The paleornithological record of the middle and upper Pleistocene of the Mediterranean islands Sardinia, Corsica, Tavolara, Mallorca, Menorca, Eivissa, Malta, Crete, Karpathos, Armathia, and Tylos is presented. Our knowledge of fossil avifaunas from islands such as Corsica, Crete, Sardinia, and Mallorca is relatively good but still incomplete. The fossil record for all of the islands includes 160 taxa. Some faunistic, evolutionary, and biogeographic considerations are discussed. The fossil Mediterranean islands avifaunas have a different species association in comparison with the modern avifaunas on the same islands and a greater number of endemic forms than today. The fossil island avifaunas lack species of the Galliformes (with the exception of *Coturnix coturnix*), Laridae, and *Passer*. A number of bird species recorded as fossils do not now occur in the Mediterranean avifaunas. The lack of some of these species has been attributed to climatic changes. Other species disappeared after the arrival of *Homo sapiens*. Endemic insular taxa have been identified in the orders Accipitriformes, Strigiformes, Anseriformes, and Passeriformes and perhaps also among the Gruiformes and Columbiformes. Changes in body size of the raptors seems related to the supply of small mammals found in the different islands. Recent extinction and local disappearance of some bird species are recorded. The extinctions and local disappearances affected species living in cold climates, large endemic species, endemic birds of prey, large and non-endemic birds of prey, some corvid species, and *Puffinus puffinus*.

RESUM. Es presenta el registre paleornitològic del Pleistocè medi i superior de les illes mediterrànies Sardenya, Còrsega, Tavolara, Mallorca, Menorca, Eivissa, Malta, Creta, Karpathos, Armathia i Tilos. El nostre coneixement de les faunes d'ocells fòssils d'illes tals com Còrsega, Creta, Sardenya i Mallorca és relativament bó, tot i que encara incomplet. Es presenten algunes consideracions faunístiques, evolutives i biogeogràfiques. Les avifaunes mediterrànies illenques fòssils tenen una associació d'espècies diferent de la que es troba a les faunes recents i contenen més formes endèmiques que les actuals. Les avifaunes fòssils illenques estan mancades de Galliformes (llevat de *Coturnix coturnix*), Laridae i *Passer*. Un cert nombre d'espècies d'aus registrades com a fòssils no es troben actualment a l'avifauna mediterrània. N'hi ha algunes que no hi són degut a canvis climàtics. Altres espècies varen desconparèixer rera l'arribada de *Homo sapiens*. S'han identificat taxa insulars endèmics als ordres Accipitriformes, Strigiformes, Anseriformes i Passeriformes, i tal volta també entre els Gruiformes i els Columbiformes. Els canvis en la talla corporal dels rapinyaires semblen estar relacionats amb l'oferta de preses microteriològiques que es donava a les diferents illes. S'han registrat extincions recents i descompareixences locals d'algunes espècies d'ocells. Aquestes han afectat, essencialment, les espècies típiques de climes freds, les espècies endèmiques grans, les aus de presa endèmiques, les aus de presa no endèmiques de talla corporal gran, algunes espècies de còrvids i *Puffinus puffinus*.

Key words: Pleistocene, Mediterranean, avifauna, evolution, biogeography, fossil birds.

INTRODUCTION

The Mediterranean Sea is a closed basin of 3,081,880 km² bordered by the continents of Europe, Africa, and Asia (Fig. 1). It contains more than 2,000 islands and islets that range in area from a few square meters to 25,708 km² (Sicily). The geological history of the Mediterranean is complex. During the Messinian, the alpine orogeny caused the closure of the Strait of Gibraltar and, as a consequence, the Mediterranean basin dried out (Hsü et al., 1973). In the western Mediterranean the desiccation was presumably complete or nearly complete. In the eastern Mediterranean, an area that was tectonically fairly active during the Pliocene and the Pleistocene, the extent of desiccation is still unknown. The opening of the Strait of Gibraltar toward the end of the Messinian, 5.5 million yr ago, resulted in the isolation of the islands and produced the emergence of the present configuration of the western Mediterranean.

Most Mediterranean islands were probably colonized by Neolithic people about 8,000 yr ago (Cherry, 1981). Earlier records of man on Mediterranean islands are scarce. Some islands, e.g., Tylos, were visited sporadically by Paleolithic man, and Corsica and Sardinia seem to have been inhabited by an endemic Paleolithic form of the genus *Homo* Linnaeus 1758 (Spoor and Sondaar, 1986; Sondaar, 1987). Recently, Simons (1988) reported the remains of a possible Paleolithic man associated with an endemic fauna, including *Phanourios minutus* (Cuvier 1824) in Cyprus. Sicily was connected to the mainland during the upper Pleistocene, allowing both a continental fauna and Paleolithic man to move onto the island.

Our present knowledge of the vertebrate faunas, and especially of the avifaunas that inhabited the Mediterranean islands before the arrival of *Homo sapiens* Linnaeus 1758, is very incomplete. The present study presents a summary of the paleornithological record of the middle and upper Pleistocene on the 11 isolated Mediterranean islands known to date to produce

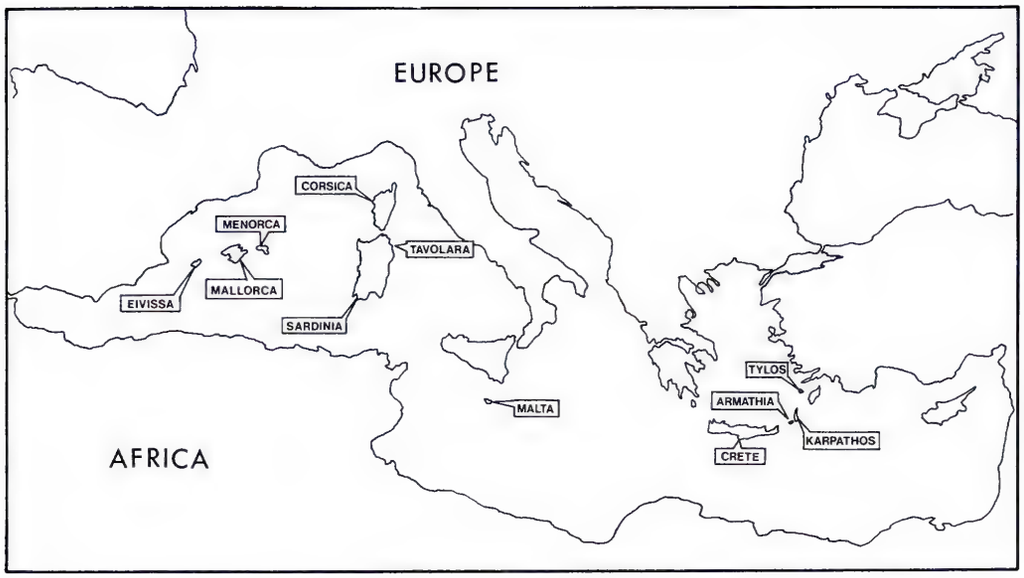

Figure 1. Map of the Mediterranean islands producing the paleoavifaunas considered in this paper.

fossil birds. Later, we describe some characteristics of the Pleistocene island avifaunas.

THE RECORD

This study is confined to the avian species known from the middle and upper Pleistocene, excluding those that have been found in association with *Homo sapiens* on various Mediterranean islands (Mallorca: Uerpmann, 1971; Levanzo: Cassoli and Tagliacozzo, 1982; Malta: various data from Lambrecht, 1933; Sicily: Regalia, 1907). The following insular paleoavifaunas from the Mediterranean are, therefore, excluded: those of the Pliocene–Quaternary boundary of Mallorca and Menorca (Mourer-Chauviré et al., 1977; Alcover et al., 1981), a Pliocene fauna of Eivissa (Alcover et al., 1981; Alcover and Agusti, 1985; and new unpublished findings), the paleofaunas of the Pliocene islands of Gargano (Ballmann, 1973, 1976), and the paleofaunas of the Miocene islands of Tuscany (Portis, 1884, 1889).

Also, this study is confined to paleoavifaunas of those islands that were not connected to the continent during the middle and/or upper Pleistocene. This includes the paleoavifauna of the islands of Sardinia, Corsica, Mallorca, Menorca, Eivissa, Crete, Karpathos, Tylos, Malta, Armathia, and Tavolara (see Table 1). Data from the first eight islands are mostly, and in some cases completely, our own, published or unpublished. References are cited in those instances where the presence of a species has not been confirmed by one of the authors.

The upper Pleistocene avifaunas of Palmaria (Regalia, 1893, 1896, 1900) and Pianosa (Caterini, 1921; Stehlin, 1928) are excluded from this study because these islands are separated from the continent by shallow sea channels (less than 20 m and 100 m deep, respectively) and were probably joined to the continent at various times during the middle and upper Pleistocene (for more information about the island of Pianosa, see Azzaroli, 1978). Also, the fossil bird bones from Palmaria are lost (Delle Cave et al., 1984), which makes it impossible to verify their identification. The paleoavifauna of Sicily is excluded because it was connected to the mainland during the upper Pleistocene.

The avifauna of the middle and upper Pleistocene on the Mediterranean islands has been the subject of numerous studies. There are references to the fossil birds of Mallorca and/or Menorca in the works of Bate (1928), Lambrecht (1933), Villalta (1964), Ballmann and Adrover (1969), Adrover (1972), Pons and Roca (1974), Mourer-Chauviré et al. (1975, 1977, 1980), Alcover et al. (1981), Reumer (1982), Northcote and Mourer-Chauviré (1988), and Florit and Alcover (1987).

The paleoavifauna of Eivissa was first dealt with by Moyà et al. (1984), Alcover and Muntaner (1985), and, more extensively, Florit et al. (1989). Suriano (1980) and Weesie (1982, 1987a, 1987b) studied the paleoavifauna of Crete; the latter also studied that of Karpathos (Weesie, 1984).

The fossil birds of Corsica have been studied by Lydekker (1891b), Newton (1921), and Mourer-Chauviré and Weesie (1986). The latter also worked on the fossil birds of Sardinia, as did Wagner (1833), Giebel (1847), De La Marmora (1857), Malatesta and Settepassi (1954), Malatesta and Suriano (1970), and Mourer-Chauviré (in Ulzega and Ozer, 1980).

The fossil birds of Malta have been studied by Parker (1865, 1869), Adams (1877), Lydekker (1890, 1891a), Bate (1916a, 1920), Despott (1927), Lambrecht (1931, 1933), Fischer and Stephan (1974), Olson (1976), Harrison and Cowles (1977), and Northcote (1982a, 1982b). Newton (1921) presents some data on the fossil birds from Kythira, a small island near the Peloponesous with a fossil mammalian fauna that reveals an overseas colonization by the pendel route (Dermitzakis and Sondaar, 1979).

The only data available from Armathia, a small island close to Kasos, South Aegean island arc, have been published by Pieper (1984), while the Quaternary avifauna of the island of Tavolara, a satellite of Sardinia, has been studied by Lydekker (1891b), Shufeldt (1896), Regalia (1897), and Mayaud and Schaub (1950).

The taxonomic modifications proposed by Brodkorb (1963, 1964) have been provisionally accepted [*Puffinus eyermani* Shufeldt 1895 becomes synonymous with *Calonectris diomedea* (Scopoli 1769); *Cygnus equitum* Bate 1916 is provisionally transfered to the genus *Anser* Brison 1760; and *Strix melitensis* Lydekker 1891 is transfered to the genus *Tyto* Billberg 1828]. We also follow Olson (1976) regarding *Scolopax ghardalamensis* Fischer and Stephan 1974, which is synonymized with *Coturnix coturnix* (Linnaeus 1758).

Not included in this study are the findings of Giebel (1847), Shufeldt (1896), Newton (1921), Wagner (1833), and De La Marmora (1857) because the taxonomic determinations made by these authors are in need of revision. Also excluded are the dubious determinations presented by Fischer and Stephan (1974). Taxonomic determinations at supraspecific level have been considered only if they were made by the authors of the present study.

Excluded as well are the observations of Lydekker (1891b) with respect to *Bubo* sp. cf. *B. africanus* (Temminck 1821) (mentioned as *Bubo* cf. *cinerascens* Guarin-Maneville 1843) and to *Coracias* sp. cf. *C. abyssinica* Hermann 1783. Lydekker (1891b) believed that the fossil faunas of the Mediterranean islands were of African origin, but it has become clear that this is not the case (e.g., Dermitzakis and Sondaar, 1979). We think that in the first case the fossils may represent the recently described endemic species *Bubo insularis* Mourer-Chauviré and Weesie 1986, whereas in the second case the fossils may represent *Coracias garrulus* Linnaeus 1758. Lydekker (1891b) likewise thought that the mammalian fauna of various Mediterranean islands (Malta, Sicily, Crete) was of African origin, and he tried to discover affinities between the fossil birds of Sardinia and the African avifauna. The Sardinian fossil bones attributed by Malatesta and his colleagues (Malatesta and Settepassi, 1954; Malatesta and Suriano, 1970) to *Bubo bubo* Linnaeus 1758 may in fact belong to *Bubo insularis;* thus, the former species has been listed with reservation. Furthermore, we think that the material attributed to *Columba melitensis* Lydekker 1891 should be reexamined in the future. *Strix aluco*? Linnaeus 1758 from the middle Pleistocene of Mallorca (Ballmann and Adrover, 1969) probably represents *Tyto balearica* (see Mourer-Chauviré et al., 1980), and for this reason it has not been included in our record.

The identifications of *Nucifraga caryocatactes* (Linnaeus 1758) from the middle Pleistocene of Mallorca (Mourer-Chauviré et al., 1977) and *Pica pica* (Linnaeus 1758) from the middle and upper Pleistocene of Mallorca (Ballmann and Adrover, 1969; Alcover et al., 1981) should be reconfirmed as well. Each of these species appears in the record of Mallorcan fossils based upon identification of either the bones of the forelimb and the shoulder girdle or the bones of the hindlimb and of the pelvic girdle; in no case are both fore- and hindlimbs and both girdles present. We think that the Mallorcan fossil material attributed to *Nucifraga caryocatactes* and *Pica pica* may in fact represent a new species of the family Corvidae.

Finally, we have excluded from this study the observation made by Lambrecht (1933) of *Corvus corax* Linnaeus 1758 from Mallorca. *Corvus corax* is a species commonly found as fossils, but it has not been encountered among the approximately 1,500 fossil bird bones exhumed on Mallorca since Lambrecht's time. We think that the species was absent from Mallorca during the Pleistocene.

The 11 islands considered in this study have provided a record of 160 taxa (species or groups of species). The best inventories are those for Corsica (74 taxa), Crete (67 taxa), Sardinia (46 taxa), Mallorca (41 taxa), and Eivissa and Malta (21 taxa each). The paleoavifaunas come exclusively from karst deposits of caves and fissures. Because of taphonomic and methodological factors, the species associations found probably correspond only partially to the avifaunas that actually lived on the islands before the arrival of *Homo sapiens.*

The paleofaunas from karst deposits tend to have a poor representation of ciconiiform species. This may be because the majority of the members of the order Ciconiiformes rarely leave the vicinity of fresh water. Furthermore, the large species within this order are not very attractive prey species for most avian raptors and, thus, would not have been carried into caves to be eaten. The karst deposits we studied had a poor representation of some families of small passeriforms. For instance, the Sylviidae are very poorly represented in the record. This may be because of the extreme fragility of their bones. On the other hand, we encountered a good representation of medium-sized and large species of the Passeriformes. The Corvidae, for instance, are well represented in our record. Their robust bones have a good chance to fossilize, and various species of the family Corvidae frequently breed and live in rocky shelters such as the entrances of caves.

Some species of *Turdus* Linnaeus 1758 are also numerically well represented. They also have robust bones, and they are, together with some species of the family Corvidae, regular prey species of birds of prey that may have brought them into the caves.

The orders Accipitriformes and Strigiformes have a good representation in the karst deposits. A high proportion of avian raptors of these orders is a common characteristic of fossil avifaunas from caves and fissures (e.g., Weesie, 1987b).

Another factor influencing the species composition of our list is the identifiability of the fossil bones. For example, the osteology of many small passeriform species is very uniform; most diagnostic characters are found in the skull. As a consequence, these species are underrepresented in our record.

The fossil record of the Mediterranean islands reflects these taphonomic and methodological biases. Nevertheless, a comparison of the fossil record of the different islands with their Recent avifauna, and with the fossil avifaunas from Europe and other islands in the world, makes it possible to deduce some of the ecological conditions that prevailed in the islands in the middle and upper Pleistocene and to draw some conclusions about the evolution and biogeography of insular species.

FAUNISTIC, EVOLUTIONARY, AND BIOGEOGRAPHICAL CONSIDERATIONS

Two main characteristics of the Mediterranean island paleoavifaunas are (1) their different species composition in comparison with the modern avifaunas on the same islands, and (2) the presence of a greater number of endemic forms than today.

COMPARISON OF THE FOSSIL AND RECENT SPECIES ASSOCIATIONS

A striking characteristic of the fossil island avifaunas is the absence of galliform species (with the exception of *Coturnix coturnix*). This is in sharp contrast to the majority of Quaternary avifaunas from caves on the European continent that are dominated by members of this order (Lambrecht, 1933), most of which were probably deposited in the caves by birds of prey. The majority of the galliform species are essentially sedentary and fly only short distances (the only exception in the European avifauna is *C. coturnix*). For this reason, they do not cross the sea channels that separate the islands from the continent, except for *C. coturnix*, which was even abundantly represented in some insular fossil avifaunas (e.g., Tavolara). On islands outside the Mediterranean [Canary Islands (Alcover, unpubl.), Madeira (Pieper, 1985)], endemic forms within the genus *Coturnix* have evolved. On the Mediterranean islands, no endemic forms of *Coturnix* evolved, probably because of the migratory habits of *C. coturnix*.

Table 1. The occurrence of avian species in the paleofaunas of the Mediterranean islands. The following designations have been used. (a) If the fossil material may belong to more than one species, the names of these species are separated with a slash (/). (b) Some new, undescribed forms have been included. These are identified at the generic or the family level. (c) The designation "cf." indicates that the characteristics observed in the fossils coincide with those of the taxon to which they are attributed, but that these characteristics do not supply all the information necessary for positive identification. (d) The designation "aff." indicates that not all of the characteristics of the fossil bones coincide with those of the taxon to which they are attributed. This designation indicates only that the fossil has some similarity to the named species.

	Sardinia	Corsica	Tavolara	Mallorca	Menorca	Eivissa	Malta	Crete	Karpathos	Armathia	Tylos
Procellariidae											
Calonectris diomedea		X[5]	X[5]			X					
Puffinus (p.) mauretanicus						X					
Puffinus (p.) yelkouan			X[5]				X				
Sulidae											
Morus bassana								X[10]			
Phalacrocoracidae											
Phalacrocorax aristotelis	X[8]	X		X		X		X			
Ciconiidae											
Ciconia ciconia	X										
Anatidae											
Branta leucopsis							X[4]				
Branta bernicla				X			X[4]				
Branta ruficollis								cf.			cf.
Anser albifrons	cf.							X[10]			
Anser erythropus		X				aff.					
Anser equitum							X[4]				
Cygnus cygnus							X[4]				
Cygnus olor	cf.[6]										
Cygnus falconeri							X[1,4]				
Tadorna tadorna		X									
Anas platyrhynchos	X[6]	X									
Anas crecca		X		X							
Anas penelope		X						X			
Anas acuta	cf.										
Anas querquedula	X[6]							X			
Anas angustirostris							X[4]				
Aythya fuligula		X									
Accipitridae											
Milvus milvus	X[8], cf.[2]										
Milvus migrans		X									
Accipiter gentilis	X	X						X			
Accipiter nisus		X		X				cf.			
Buteo lagopus	cf.										
Buteo buteo	X	X						X			
Hieraetus fasciatus							X[4]				
Aquila heliaca	cf.	cf.									
Aquila chrysaetos	X	X		X		X	?[3]	X			
A. c. simurgh								X			
Haliaeetus albicilla	X	X						X	X		
Circus macrourus	X[8]										
Circus aeruginosus		X									
Circus cyaneus	cf.[8]										
Gypaetus barbatus	X[6,8]			*				X			
Aegypius monachus	X[2,8]			*				X			
Gyps fulvus	X	X						X			
Gyps melitensis							X[1,4]	X			

Table 1. Continued.

	Sardinia	Corsica	Tavolara	Mallorca	Menorca	Eivissa	Malta	Crete	Karpathos	Armathia	Tylos
Falconidae											
Falco peregrinus	X[8]	X						X			
Falco subbuteo		X						X			
Falco eleonorae				X		X		X			X
Falco naumanni		X									
Falco tinnunculus	X	X		X		X		X			X
Falco sp.				X							
Phasianidae											
Coturnix coturnix	X	X	X[2]	X		X	X[9]	X			
Gruidae											
Grus primigenia				X		X					
Grus melitensis							X[1,4]				
Rallidae											
Rallus aquaticus		X							X		
Porzana porzana		X		X				X			
Porzana parva		X									
Porzana pusilla		X									
Crex crex		X									cf.
Gallinula chloropus		X						X			
Fulica atra								X			
Glareolidae											
Glareola pratincola/nordmanni								X			
Otitidae											
Otis tarda						X	X[4]				
Otis tetrax		X					X[4]				
Charadriidae											
Vanellus vanellus		X									
Scolopacidae											
Calidris canutus								X			cf.
Tringa erythropus		X									
Tringa totanus		X									
Limosa limosa	X[8]	X									
Scolopax rusticola	X	X		X				X			
Gallinago gallinago	X[6]	X									
Gallinago media		X									
Alcidae											
Fratercula artica		X									
Columbidae											
Columba palumbus	X	X						X			
Columba oenas	X							X			
Columba livia	X[6,8]	X	cf.[2]	X	X	X		X	X		
Columba oenas/livia	X	X[2]		X				X	X		X
Streptopelia turtur	X[6]										
Streptopelia turtur/decaoto											X
Cuculidae											
Cuculus canorus		X									
Tytonidae											
Tyto alba	X[8]						X[9]	X	X		
Tyto melitensis							X[1,3,4]				
Tyto balearica				*	*						

Table 1. Continued.

	Sardinia	Corsica	Tavolara	Mallorca	Menorca	Eivissa	Malta	Crete	Karpathos	Armathia	Tylos
Strigidae											
Bubo insularis	X	X	cf.[2]								
Bubo bubo	?[6,8]										
Asio otus		X									
Asio flammeus	X					X		X			
Otus scops	X	X		X		X, aff.	X[9]	X			X
Aegolius funereus								X			
Athene noctua	aff.			X					X		X
Athene cretensis								X		X[11]	
Ketupa zeglonensis								X			
Caprimulgidae											
Caprimulgus europeus		X			X			cf.			
Apodidae											
Apus apus/pallidus				X		X			X		
Apus melba	X	X		X					X		
Meropidae											
Merops apiaster		X									
Coraciidae											
Coracias garrulus		X	?[2]								
Upupidae											
Upupa epops				X							
Picidae											
Jynx torquilla				X							
Picus viridis	cf.										
Dendrocopos major		X									
Dendrocopos leucotos								X			
Alaudidae											
Calandrella brachydactyla								cf.			
Melanocorypha calandra				X							
Galerida cristata		X									
Lullula arborea	cf[2]	X									
Alauda arvensis						X					
Hirundinidae											
Hirundo rupestris				X		X					
Hirundo rustica	cf.[2]	X									
Hirundo daurica								cf.			
Hirundo rustica/daurica							X[9]				
Delichon urbica											X
Motacillidae											
Motacilla alba				X							
Anthus spinoletta		X									
Laniidae											
Lanius collurio		X									
Lanius minor		X		X		X					
Lanius excubitor		X									
Troglodytidae											
Troglodytes troglodytes				X							
Prunellidae											
Prunella collaris	X			X				X	X		

Table 1. Continued.

	Sardinia	Corsica	Tavolara	Mallorca	Menorca	Eivissa	Malta	Crete	Karpathos	Armathia	Tylos
Muscicapidae											
Acrocephalus paludicola		X									
Sylvia atricapilla		X									
Sylvia sp.											X
Muscicapa striata								cf.			
Saxicola rubetra		X									
Oenanthe hispanica								X			
Oenanthe sp.									X		
Monticola solitarius								cf.			
Phoenicurus phoenicurus		X									
Erithacus rubecula		X						cf.			
Luscinia megarhynchos		X									
Turdus spp.	X	X		X		X	X[9]	X			X
Zoothera dauma								cf.			
Emberizidae											
Emberiza calandra								cf.			
Emberiza cia/hortulana				X							
Emberiza cirlus		cf.									
Emberiza cirlus/schoeninclus								X			
Emberiza citrinella/hortulana								X			
Emberiza sp.				X							
Fringillidae											
Fringilla coelebs		X	cf.[2]	X							
Fringilla coelebs/montifringilla								X			
Serinus serinus			cf.[2]								
Serinus citrinella		X									
Carduelis chloris		X					X[9]	X			
Carduelis cannabina				X[7]							
Loxia curvirostra				X							
Pyrrhula pyrrhula	cf.[2]			X				cf.			
Coccothraustes coccothraustes		X	X[2]	X			X[9]	X		cf.	
Fringillidae gen. sp.				X							
Ploceidae											
Petronia petronia		X									
Sturnidae											
Sturnus vulgaris	X[8]	X					X[9]				
Sturnus vulgaris/unicolor/roseus								X			
Oriolidae											
Oriolus oriolus		X									
Corvidae											
Garrulus glandarius	X[6]							X			X
Pyrrhocorax pyrrhocorax	X[6,8]			X	X	X		X			cf.
Pyrrhocorax graculus	X	X		X				X			
Corvus monedula	X			X				X			X
Corvus corone/frugilegus	X	X	X[2]	X				X	X		
Corvus antecorax						X					
Corvus corax	X	X						X			
Corvidae gen. sp.				X							

(1) Lydekker, 1890; (2) Lydekker, 1891b; (3) Lydekker, 1891a; (4) Bate, 1916a; (5) Mayaud and Schaub, 1950; (6) Malatesta and Settepassi, 1954; (7) Ballmann and Adrover, 1969; (8) Malatesta and Suriano, 1970; (9) Fischer and Stephan, 1974; (10) Suriano, 1980; (11) Pieper, 1984; (*) presence inferred.

The absence of species of *Alectoris* Kaup 1829 from the paleoavifaunas may be similarly explained. The first records of partridges on Mediterranean islands coincide with the appearance of *Homo sapiens* (e.g., Cassoli and Tagliacozzo, 1982). It is therefore highly probable that the present distribution of partridges on the Mediterranean islands is related to the presence of man. Recent endemic subspecies of *Alectoris* have been recognized on some of the Mediterranean islands (e.g., *A. rufa corsa* in Corsica, *A. graeca whitakeri* in Sicily). The process of differentiation that has led to the formation of these subspecies may have been rather short and recent (Moreau, 1966; Blondel, 1985).

Another remarkable characteristic of the fossil avifaunas from the Mediterranean islands is the absence of species of the family Laridae. Abundant fossil remains of larid species have been found on many islands in other parts of the world [e.g., Bahamas (Olson and Hilgartner, 1982), St. Helena (Olson, 1975)] and in continental coastal deposits (e.g., de Muizon, 1981). The absence of larid fossils from the Mediterranean islands suggests a scarcity, or total lack, of gulls in the Mediterranean during the middle and upper Pleistocene.

The absence of *Passer* Brisson 1760 in the fossil record of the Mediterranean islands is also noteworthy. Species of *Passer* are very abundant on these islands today, and they are the prey of various avian raptors. Their absence from the fossil record suggests that they were nonexistent, or extremely rare, on the Mediterranean islands before the arrival of *Homo sapiens.*

In contrast to the previous examples, a number of bird species recorded as fossils do not occur in the Recent Mediterranean avifauna. Some of these bird species presently occur farther to the north, and it is supposed that a change in climate is the reason for this change in distribution.

Morus bassanus (Linnaeus 1758), found as fossil on Crete (Suriano, 1980), today breeds about 1,000 km to the north of the island on the European Atlantic coast. Because this species only comes ashore to breed, the fossil evidence may indicate that it bred during the Pleistocene on Crete (Weesie, 1987b).

Among freshwater birds, various species are listed in the record that at present breed or winter in more northern regions. This applies to *Cygnus cygnus* (Linnaeus 1758) and the species of *Branta* Scopoli 1769 [*B. leucopsis* (Bechstein 1803) on Malta, *B. bernicla* (Linnaeus 1758) on Mallorca and Malta, *B.* sp. cf. *B. ruficollis* (Pallas 1769) on Crete and Tylos] that breed in the rocky high tundra and on the islets off the Arctic coast. At present these species spend the winter well to the north of the sites where their fossil remains have been found.

The remains of *Anser* sp. aff. *A. erythropus* (Linnaeus 1758) are of adult and very young birds, which may indicate that this species bred on Eivissa in the Pleistocene. *Anser erythropus* currently breeds in the extreme north of Norway. Most of the remains of *Branta* sp. cf. *B. ruficollis* from Tylos belong to young birds.

The following land birds breed or winter north of the sites from which they have been recorded as fossils: *Buteo lagopus* (Pontoppidan 1763), *Gallinago media* (Latham 1787), *Zoothera dauma* (Latham 1790), and *Aegolius funereus* (Linnaeus 1758). *Dendrocopus leucotus* (Bechstein 1803), *Pyrrhula pyrrhula* (Linnaeus 1758), *Prunella collaris* (Scopoli 1769), and *Pyrrhocorax pyrrhocorax* Linnaeus 1758 currently breed in higher, colder zones, up to the snow limit. The presence of these bird species on the Mediterranean islands in the middle/upper Pleistocene indicates that colder climatic conditions existed in this area at the time the bird bones were deposited. During glacial periods, there was apparently a latitudinal displacement to the south of the distribution of species that today are considered more northern European species. The species that bred in the high mountains of the Mediterranean probably underwent a vertical displacement of their breeding zones (Moreau, 1955) during the glacial periods. The Mediterranean basin may have served as a refuge for those species deprived of suitable habitats farther north or in the mountains. The withdrawal of glacial ice from Europe allowed the avian species more adapted to a cold climate to return to more septentrional or higher elevation areas.

For a number of other bird species listed in the fossil record, their present absence from the islands is probably not related to climatic factors. Into this category fall *Aquila* sp. cf. *A. heliaca* Savigny 1809 (at present absent from Corsica and Sardinia), *A. chrysaetos* (Linnaeus 1758) (absent from Mallorca and Eivissa), *Gypaetus barbatus* (Linnaeus 1758) (absent from Mallorca), *Haliaeetus albicilla* (Linnaeus 1758) (absent from Crete and Karpathos), *Coccothraustes coccothraustes* (Linnaeus 1758) (absent from Mallorca), *Ketupa zeylonensis* (Gmelin 1788) (absent from Crete), and *Pyrrhocorax pyrrhocorax* (absent from Mallorca, Menorca, and Eivissa). The presence of these species in the fossil record helps to identify primitive distributions (plesiochories) and demonstrates that the present fragmented distribution of these species is of fairly recent origin. It is not easy to explain the recent local extinctions of these species. They possibly ceased to exist on the various Mediterranean islands after the colonization by *Homo sapiens.* The large birds of prey may have died out on the islands either as a result of direct hunting by man or as a result of the influence of man on their food resources.

ENDEMIC PLEISTOCENE BIRDS FROM THE MEDITERRANEAN

Endemic species of birds have evolved on the Mediterranean islands, as on other islands of the world. The number of endemic species is, however, far less than that found on various archipelagos or isolated islands of the world located at great distances from continents. On the Mediterranean islands, endemic insular taxa have been identified in the orders Accipitriformes, Strigiformes, Anseriformes, and Passeriformes and perhaps also among the Gruiformes and Columbiformes.

Accipitriformes and Strigiformes

Most known endemic forms of the Mediterranean islands evolved among the birds of prey. *Aquila chrysaetos simurgh* Weesie 1987 was thought to be adapted to feed on the endemic deer of Crete. *Tyto balearica* Mourer-Chauviré, Alcover, Moyà, and Pons 1981 was a predator of a large dormouse, *Hypnomys* Bate 1918, on the Balearic Islands. Recently, remains of a large owl have been found in several deposits of the Iberian Peninsula and the south of France that may represent *Tyto balearica* (Mourer-Chauviré and Sanchez, in prep.). There is also *Bubo insularis* in Corsica and Sardinia, probably adapted to eat the pika *Prolagus sardus* (Wagner 1829), and *Athene cretensis* Weesie 1982 in Crete, adapted to feed on the murid *Mus minotaurus* Bate 1942.

It would be interesting if new fossil remains of *Aquila* sp. cf. *A. heliaca* were found in Corsica and Sardinia in the future. *Aquila heliaca* is an essentially theriophagic species that feeds mainly on rabbits on the continent (Valverde, 1967). It may be presumed that on islands certain changes in size and body proportions of eagles have taken place in response to the size of their prey species.

It is interesting to note that on those islands where endemic owls have been found, a change in body size has normally taken

place in only one species. Furthermore, it has not always been the same genus from which the endemic form has originated. Arnold (1976), when studying cases of gigantism in insular sauria, suggested that on small islands the development of one giant form would prevent the emergence of another giant species. The genus to which the giant form belongs is probably determined by historical factors; i.e., the first species of sauria to colonize an island could be the one to monopolize the resources and to develop gigantism. Something similar may have happened to the species of owls. Once an endemic form is established on an island and exploits its specific resources, it would be difficult for another species to develop similar adaptations and occupy the same niche. For this reason, endemic species of *Athene* Boie 1822 may have evolved on some islands, and endemic species of *Tyto* and *Bubo* on other islands. Only on larger islands might it be possible for various species of the Strigiformes to evolve by either increasing or decreasing their body size as an adaptation to feeding on different resources. The limited range of resources available on smaller islands would probably only allow the evolution of a single endemic strigiform species.

It is important to emphasize that a particular strigiform species does not always change its size in the same way. For example, in the genus *Tyto* there are giant forms on many islands in the world (e.g., Cuba, Gargano, Mallorca, Menorca), but there are also dwarf forms on other islands (e.g., the Canary Islands, the Galápagos).

Anseriformes

In the order Anseriformes, there is a species, *Cygnus falconeri* Parker 1865, that has abandoned the aquatic habits of its ancestors for a semi-terrestrial way of life. Its anatomical adaptations to this way of life have been described by Northcote (1981–1983, 1982b). It was a large swan (approximately 16 kg), probably flightless, with a very robust hindlimb and particularly short feet. The remains of *Anser equitum* (Bate 1916) from Malta should be reexamined. [See Northcote, 1988; this volume.—Ed.]

Gruiformes

Grus melitensis Lydekker 1890 was described from Malta. This is a crane of the same size as *Grus antigone* (Linnaeus 1758) and *G. primigenia* Milne-Edwards 1869, and morphologically it varies from the latter only in a few details. Studies are currently under way regarding the specific identity of all these forms (Mourer-Chauviré et al., 1975; Harrison and Cowles, 1977; Northcote 1982a, 1984). It seems improbable that an endemic, volant species of *Grus* lived only on Malta.

Ralliformes

Although endemic insular species of ralliforms are found in numerous islands of the world, they are unknown from the Mediterranean. Usually, insular species of the family Rallidae are flightless forms, adapted to a more terrestrial way of life than their continental counterparts. They are generally found on mammal-free islands at great distance from the continent. The reason for the absence of endemic insular species of rails from the Mediterranean may lie in the migratory habits of most members of this order.

Passeriformes

Endemic forms have originated in at least four families of the order Passeriformes: Corvidae, Sylviidae, Sittidae, and Fringillidae. So far, fossil endemic taxa of the family Corvidae have been found on the islands of Mallorca (Corvidae n. sp.; Alcover, in prep.), possibly Eivissa [*Corvus antecorax* Mourer-Chauviré 1975 (n. ssp.?); Florit et al., in press], and possibly Crete [*Garrulus glandarius* (Linnaeus 1785) (n. ssp.?); Weesie, 1987b]. Of the families Sylviidae and Sittidae, no fossil endemic forms are known. Nevertheless, Recent *Sitta whiteheadi* Sharpe 1884 from Corsica is an endemic species adapted to living in the *Pinus nigra* Arnold 1785 forests. The genus *Sylvia* Scopoli 1769 has radiated in the Mediterranean area, and some of its Recent species are exclusively insular, e.g., *Sylvia sarda* Temminck 1820 (on the islands of the western Mediterranean) and *Sylvia melanothorax* Tristam 1872 (on Cyprus). A recent find of a very robust bill from the upper Pleistocene of the island of Mallorca (with Menorca the most isolated island of the Mediterranean) has revealed the presence of a new fringillid species, the only record of an endemic species of the family Fringillidae from the Mediterranean islands.

EXTINCTIONS AND DISAPPEARANCES FROM THE MEDITERRANEAN ISLANDS

The extinctions and immigrations of bird species in the Mediterranean islands in the middle and upper Pleistocene were nonrandom events, and extinction did not affect all the endemics in the same way. With regard to the faunas that concern us, the cases of extinction and/or disappearances that have taken place have affected the following groups.

1. The occurrence and disappearance of a certain number of species from the region was probably directly tied to changes in climate.

2. Large, endemic, flightless species are particularly susceptible to extinction after human colonization of islands (Martin and Klein, 1984; Olson and James, 1982, 1984). In the case of Mediterranean avifaunas, only one flightless taxon is known—*Cygnus falconeri* of the upper Pleistocene of Malta. We have no evidence for the causes of its extinction, but human colonization of the island may have played a role.

3. Most endemic birds of prey probably depended on endemic mammals for prey. The disappearance of the latter as a result of the activities of man and/or to the fauna he brought with him may have meant the concomitant disappearance of raptorial birds. Also, direct hunting of the endemic species may have played a role. This is certain for the following group.

4. Large, non-endemic birds of prey disappeared from several islands, e.g., the disappearance of *Haliaeetus albicilla* and *Aegypius monachus* (Linnaeus 1758) from Crete and *Aquila chrysaetos* from Mallorca). Of the non-endemic raptors, it was mostly the large species that disappeared. According to Blondel (1979), the ecological niches of birds of prey on islands are occupied by smaller species than on the mainland. This may be true for the present, but this does not appear to apply to the upper Pleistocene faunas. The insular paleofaunas of the upper Pleistocene contained not only species of birds of prey of identical size as those of continental faunas, but they also contained even larger species, e.g., *A. c. simurgh* on Crete.

5. The extinction or disappearance of species of the family Corvidae has occurred in Mallorca, Menorca, Eivissa, and Sardinia. The disappearance of *Pyrrhocorax graculus* (Linnaeus 1766) from Mallorca and Sardinia may be attributable to climatic changes because this species prefers a cold climate. Because the modern-day distribution of *P. pyrrhocorax* covers a large climatic range, the disappearance of *P. pyrrhocorax* from Mallor-

ca, Menorca, and Eivissa is probably not related to changes in the climate. On Eivissa, the youngest remains of *Corvus antecorax* have been found in a layer just below the layers that produced the first record of man. Therefore, we think that ecological changes caused by man may explain the disappearance of *P. pyrrhocorax* from the previously mentioned islands and also the extinction of *C. antecorax* on Eivissa.

6. Among marine birds, a major change is the disappearance of the breeding colonies of *Puffinus puffinus mauretanicus* from the island of Eivissa and of the nesting populations of *P. p. yelkouan* from Crete. The disappearance of these populations is probably related to the introduction of different species of mammals to these islands. It is well known that rats and cats can have a disastrous influence on breeding colonies of these species. At present, the largest breeding colonies of *P. puffinus* (Brünnich 1764) in the Mediterranean area are found in islets that are free of mammals.

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SWANS (*CYGNUS*) AND CRANES (*GRUS*) FROM THE MALTESE PLEISTOCENE

E. Marjorie Northcote

ABSTRACT. *Cygnus falconeri* and *C. equitum*, the largest and smallest known swans, the giant crane *Grus melitensis*, and the extant *C. c. cygnus* and *G. grus* are described from Ipswichian (Eemian) deposits of the last interglacial stage (c. 125,000 B.P.) of Malta. *Cygnus falconeri* resembled *C. c. cygnus* but had stouter leg bones and shorter, stoutef toes. Using scaling formulae, I estimate that it weighed c. 17 kg and had a wing span of c. 3 m. It probably walked well, foraged inland, and had limited flight capabilities.

Cygnus equitum had a comparatively broad body and stout bones. It resembled *C. cygnus* but had shorter distal wing bones more like those of *C. olor*. The stoutness of two cervical vertebrae and details on certain limb bones are goose-like. This swan could feed near fresh or salt water; it was probably able to fly, though it was rather terrestrial. It weighed c. 3.5 kg and had a wing span of c. 1.5 m.

Grus melitensis, the extant *G. antigone*, and the extinct *G. primigenia*, though similar in size, differ morphologically. I reassign the syntype coracoid of *G. melitensis* to *G. grus*. I refute evidence that *G. melitensis* had reduced flight capabilities. It was probably more terrestrial than *G. grus* and *G. antigone*. During the Ipswichian (Eemian), Malta was lush with vegetation; fresh water was in abundance, and there were few predators on the island.

Key words: swans, cranes, Malta, Pleistocene, Aves, evolution.

INTRODUCTION

This contribution is a synopsis of data and conclusions hitherto scattered in different papers, enriched with some new findings. I have great pleasure in dedicating it to Pierce Brodkorb, whose work has been a constant source of reference and inspiration.

Sicily and Malta were connected at various times in the Pleistocene by an isthmus or islands because of a fluctuating sea level that was often lower than now (Zammit-Maempel, 1977; Sondaar and Boekschoten, 1967). The fossils of Malta usually occur in a thin stratum (Adams, 1870). No precise dates are available for the Maltese paleoavifauna (Pedley, 1981:71) but avian fossils are often associated with, and therefore have the same date as, the extinct pygmy elephant *Palaeoloxodon melitensis* Falconer 1862. This elephant lived on Malta in a period equivalent to the Ipswichian (Eemian), the last interglacial stage of more northern countries (Sondaar, 1971), or c. 125,000 B.P. (Shotton, 1985).

The paleoavifauna is biased in favor of large water birds; three swans (*Cygnus* Bechstein 1803) and two cranes (*Grus* Pallas 1766) are discussed herein. The giant Maltese Swan, *C. falconeri* Parker 1865; the dwarf "swan-goose," *C.* (*Anser*?) *equitum* Bate 1916; and the Maltese Crane, *G. melitensis* Lydekker 1890, are extinct. *Cygnus c. cygnus* (Linnaeus 1758) and *G. grus* (Linnaeus 1758) are extant.

METHODS

For comparisons with geese, I chiefly used *Anser* Brisson 1760, which is less specialized than *Branta* Scopoli 1769 (Johnsgard, 1965) and in particular *A. anser* (Linnaeus 1758), the largest western Palaearctic goose (Cramp and Simmons, 1977). I followed Johnsgard (1974) in treating the Whooper Swan and Bewick's Swan as subspecies of *Cygnus cygnus*, viz. *C. c. cygnus* and *C. c. bewickii*. For comparisons with swans, I chiefly used *C. c. cygnus* and *C. olor* (Gmelin 1789) because of their more southern Palaearctic range. For comparisons with cranes, I used *Grus grus* and *G. antigone* (Linnaeus 1758) because of their more southern Eurasian range.

Measurement procedure is given elsewhere (Northcote, 1979b, 1981). Scaling formulae are used for estimating weight and wing span. For geometric similarity, length = $K_1 \times \text{wt.}^{0.33}$ and width = $K_2 \times \text{wt.}^{0.33}$ (Alexander, 1971); for elastic similarity, length = $K_3 \times \text{wt.}^{0.25}$ and width = $K_4 \times \text{wt.}^{0.375}$ (McMahon, 1973, 1975). Wingspan = $1.1 \times \text{wt.}^{0.33}$ for all birds (Tucker, 1977) or wingspan = *a constant* $\times \text{wt.}^{0.39}$ for swans (Alexander, 1971). Anatomical nomenclature follows Baumel (1979) and Vanden Berge (1979). Chief fossil localities are shown in Fig. 1.

Repository abbreviations are as follows: BMNHL, British Museum (Natural History), London; BMNHT, Natural History Museum, Tring; NMNHM, National Museum of Natural History, Malta; and UMZC, University Museum of Zoology, Cambridge.

DESCRIPTION

Cygnus falconeri Parker 1865

Giant Maltese Swan

Cygnus falconeri has been found on Malta at Zebbug (Parker, 1865, 1869), but the specimens are lost (Lydekker, 1890); Ghar Dalam (Bate, 1916); Mnajdra (Northcote, 1982b); Tal Gnien (BMNHL, uncatalogued specimens); and elsewhere (Howard, 1964). Available for study are a cranium fragment, parts of an ulna shaft, femora, tibiotarsi and tarsometatarsi, a complete

Figure 1. Map of Malta showing chief fossil localities (numbered).

tarsometatarsus, several complete pedal digit IIIs, and fragmentary and complete specimens of other pedal digits. Parker (1865, 1869) and Lydekker (1890, 1891) thought *C. falconeri* was goose-like. Measurements are given elsewhere (Northcote, 1982b).

UMZC 252a includes frontal bones with interorbital area and sulci glandulae nasalis, which housed the salt glands. The small size of the latter in *Cygnus falconeri* shows that it did not feed in or near salt water. The cranium lacks the frontal knob of *C. olor.*

The structure of the leg bones of *Cygnus falconeri* is that of swans but not of geese (Northcote, 1982b). Features of the ankle joint of *C. c. cygnus* and *C. olor* are related to their walking ability; the former walks more efficiently (Northcote, 1981). In *C. falconeri,* features of the ankle joint and also of the femur head are similar to those of *C. c. cygnus,* but not to those of *C. olor;* hence, the extinct swan probably walked efficiently (Northcote, 1982b). The general structure of the tarsometatarsus of *C. falconeri* is more like that of *C. c. cygnus* than *C. olor,* though this bone and the femur are stouter in the extinct bird than in *C. c. cygnus* (tarsometatarsus, $P = 0.010$; one-sided test; femur, $0.025 > P > 0.010$) (Northcote, 1982b).

A left foot, lacking only ungual phalanges, can be assembled from the fossils. The toes are shorter and stouter than in Recent swans. Phalanges 1, 2, and 3, the chief components of pedal digit III, total c. 103 mm in length. A decrease in the ratio (length of digit III : length of tarsometatarsus) indicates an increase in adaptation to terrestrial locomotion (Charig, 1972). For *Cygnus olor* and *C. c. cygnus, Anser albifrons* (Scopoli 1769), and *C. falconeri,* this ratio = 1.28, 1.08, 0.89, and 0.75, respectively. *Cygnus olor* feeds chiefly on aquatic plants, *C. c. cygnus* feeds on aquatic and land plants, and *A. albifrons* feeds chiefly on land plants (Cramp and Simmons, 1977). The ratios indicate that *C. falconeri* was even more terrestrial than the goose *A. albifrons.*

Cygnus falconeri is represented chiefly by hindlimb bones. Because they resemble those of *C. c. cygnus,* but not those of *C. olor,* the weight for *C. falconeri* was calculated using data from *C. c. cygnus;* earlier workers used data from *C. olor.* Measurements are given elsewhere (Northcote, 1982b). For weight estimations, constants were calculated using mean tarsometatarsi length and width, which are the most accurate measurements for *C. falconeri,* together with the mean weight of *C. c. cygnus* (9.72 kg; Northcote, 1981). McMahon's (1973, 1975) formulae for elastic similarity gave the closest estimate to the actual tarsometatarsus length and width of *C. c. bewickii* (conspecific with *C. c. cygnus*). Using the relevant constants and the tarsometatarsus length or width, the mean estimated weight of *C. falconeri* is 17.5 kg or 16.7 kg, respectively. Using these weights and Alexander's (1971) formula, the estimated wingspan of *C. falconeri* is 3.05 m or 3.00 m. Using Tucker's (1977) formula, wingspan is 2.83 m or 2.78 m. At c. 17 kg and c. 3-m wingspan, *C. falconeri* is the largest known swan. Birds with c. 3-m wingspan lack maneuverability (Tucker, 1977) and usually employ soaring techniques (Kokshaysky, 1977); however, swans do not soar (Pennycuick et al., 1979). Although the ulna UMZC 252a of *C. falconeri* has papillae remigiales caudales for flight feathers, *C. falconeri* probably had more limited flight capability than *C. c. cygnus.*

Cygnus equitum Bate 1916

Dwarf Maltese "Swan-Goose"

Bate (1916) named a series of fossils from Malta *Cygnus equitum.* Lambrecht (1933) and Howard (1964) also assigned them to *Cygnus,* but Brodkorb (1964) referred to them as *Anser equitum* (Bate). The type series of *C. equitum* Bate 1916,

NMNHM 20 and 21, came from Ghar Dalam, Malta. Casts, catalogued as *A. equitum* (Bate), are BMNHL A1613, A1614, and A1615. Lambrecht (1933) reported the bird from the Maltese sites Ta' Kandja, Tal Herba, Benghisa, and Kalafrana. I have found it among museum collections from several sites; the bones were unidentified or identified as *C. falconeri* or *C. equitum*. Lambrecht (1933), Brodkorb (1964), Howard (1964), and others followed Bate (1916) in stating that *C. equitum* was flightless. BMNHL A3267 from Tal Gnien includes the frontal area with right supraorbital margin, postorbital region, and occipital plane with condyle, foramen magnum, and alae tympaticae. UMZC 252a from Mnajdra includes a braincase infill with a posterior frontal fragment and the occipital plane with condyle and foramen magnum. Limb bone measurements are given elsewhere (Northcote, 1988).

Bate (1916) was correct in assigning this species to *Cygnus*. Pronounced attachment areas for ligaments and muscles indicate the presence of a comparatively long beak. The shape of the scapula, coracoid, humerus head, carpometacarpus, and proximal phalanx of the major wing digit, together with the ratios of the lengths of the chief limb bones to one another, all show *C. equitum* to be more swan-like than goose-like (Northcote, 1988). However, the stouter shape of two cervical vertebrae (Fig. 2), the presence of an impressio m. supracoracoidei on the humerus, the flaring of the lateral condyle of the femur, and the form of the trochlear groove of metatarsal IV are goose-like characters (Northcote, 1988).

Cygnus equitum resembles *C. c. cygnus*, but not *C. olor*, in having no bill knob, in the form of the proximal extremity of the humerus, in the proportions of the coracoid and of the humerus, and in the ratio femur length : humerus length (Northcote, 1988). However, the relative shortness of the carpometacarpus and phalanx proximalis digiti majoris resembles that of *C. olor*. Compared to both Recent swans, the limb bones are stouter and shorter and the sulci for the m. humerotriceps and the m. scapulotriceps, which extend the wing at the elbow, are deeper in *C. equitum* (Northcote, 1988).

The sulcus glandulae nasalis is large, suggesting *Cygnus equitum* could feed near salt water. An impressio m. supracoracoideus on the crista pectoralis indicates the ability to perform jump take-offs from level ground (Sy, 1936; Pennycuick, 1972). *Cygnus equitum* may, therefore, have taken off like geese rather than from water like swans. The goose-like characters of the femur and the tarsometatarsus previously noted also suggest that *C. equitum* was rather terrestrial. Bate (1916) stated that *C. equitum* lacked papillae remigiales caudales on the ulna and, therefore, could not fly. However, there are such papillae on the ulna, e.g., BMNHL A5225, and also on the os metacarpale majus, e.g., NMNHM Q. 102. F25; hence, primaries and secondaries, the chief flight feathers, were present (Northcote, 1988). Furthermore, the flight apparatus is not reduced. Therefore, no evidence indicates that *C. equitum* was flightless. The greater stoutness of the wing bones suggests that the wing of *C. equitum* had a thicker leading edge than in the Recent swans; the relative shortness of its distal wing bones suggests it had a rather low aspect ratio. In addition, the coracoid of *C. equitum* is the same length (c. 75 mm) as that of the larger *C. cygnus bewickii*, so the body was comparatively broad (Northcote, 1988). These body characters are associated with slower flight (McFarland et al., 1979).

Because *Cygnus equitum* resembles *C. c. cygnus*, but not *C. olor*, in structure, its weight was estimated using the weight of *C. c. cygnus* (Northcote, 1988). Constants were calculated using humerus length (the most accurate measurement in *C. equitum*).

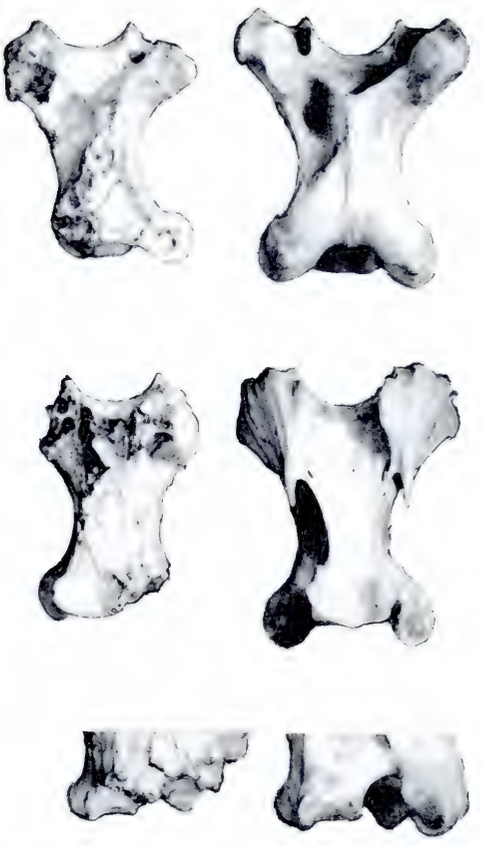

Figure 2. **Left:** Eighteenth(?) cervical vertebra of *Cygnus equitum*. **Right:** Eighteenth cervical vertebra of *C. c. cygnus*. **Top:** Dorsal view; **center:** ventral view; **bottom:** craniolateral view showing centrum. 1×.

The formula for geometric similarity gave the closest estimate to the actual humerus length of *C. c. bewickii*. Using the relevant constant and the humerus length of *C. equitum*, its mean estimated weight is c. 3.5 kg. The mean weight for *C. c. bewickii* is 6.1 kg (n = 191) (Northcote, 1981). Using Tucker's (1977) equation, the wingspan of *C. equitum* is c. 1.68 m. Using Alexander's (1971) equation, and taking into account that the wing of *C. equitum* was probably more similar in shape to that of *C. olor* than to that of *C. c. cygnus*, the wingspan of *C. equitum* is estimated to be 1.20–1.78 m. The wingspan of *C. c. bewickii* is 1.80–2.11 m (Cramp and Simmons, 1977). It appears that *C. equitum* was lighter and had a smaller wingspan than any Recent swan.

Cygnus cygnus cygnus (Linnaeus 1758)

Whooper Swan

Parker (1865, 1869) recorded *Cygnus cygnus* from Zebbug. His specimens, now lost, included the diagnostically important anterior sternum. Other specimens have come from Ghar Dalam (BMNHL 449d; Bate, 1916; Lambrecht, 1933); Mnajdra (Northcote, 1979a); Tal Gnien (BMNHL; uncatalogued fragments), and other sites (NMNHM Q/15–Q/17). The bones are the size of those of Recent *C. c. cygnus*. *Cygnus c. cygnus* occurs accidentally in the western Mediterranean but evidently lived there in the last interglacial, at which time it also lived in Britain

Table 1. Measurements (mm) of hindlimb bones of *Grus melitensis* and *G. antigone*[1]. Number of specimens in parentheses.

	Grus melitensis	*Grus antigone*
Femur		
Max. mediolat. width		
Prox.	c. 36[2]	29.3–34.9 (8)
Dist.	c. 35.3[3]	32.6–33.3 (8)
Max. craniocaudal width		
Condylus lateralis	c. 31[3]	c. 32.4
Mediolat. med. shaft width	c. 21.8[3]	c. 18.8
Tibiotarsus		
Max. mediolat. dist. width	24.0–25.5 (3)[2] 24.6–27.9 (10)[4]	23.9–28.6 (8)
Tarsometatarsus		
Max. mediolat. width		
Prox.	28.1, 28.6[2]	27.1–33.3 (8)
Dist.	32.0[5]	26.1–31.5 (8)
Phalanx prox. dig. sec.		
Max. mediolat. width		
Prox.	9.5[6]	10.3–11.1 (4)
Dist.	6.9[6]	7.3–8.0 (4)
Mediolat. med. shaft width	5.7[6]	5.7–6.5 (4)
Max. length	33.6[6]	40.0–42.5 (4)

[1] Specimens in BMNHT, UMZC.

[2] UMZC 252a.

[3] BMNHL A5220.

[4] From Harrison and Cowles (1977).

[5] BMNHL 49358.

[6] BMNHL 49324e.

(Northcote, 1979a). In the last glacial, it was widespread in Europe (Brodkorb, 1964).

Grus melitensis Lydekker 1890

Maltese Crane

Lydekker (1890, 1891) based *Grus melitensis* on fossils from Zebbug comprising the cranial half of a coracoid (BMNHL 49365), distal extremities of a tibiotarsus (BMNHL 49361) and tarsometatarsus (BMNHL 49358), part of a pelvis (BMNHL 49322m) and of a tibiotarsus (BMNHL 49322n), and a pedal phalanx (BMNHL 49324e). From Tal Gnien have come distal fragments of a tibiotarsus and a proximal tarsometatarsus (Harrison and Cowles, 1977) and a distal part of a femur (BMNHL A5220) (Northcote and Mourer-Chauviré, 1988); from Mnajdra have come fragments of a cranium, proximal femur, and proximal and distal tibiotarsus and tarsometatarsus, (UMZC 252a) (Northcote, 1979a, 1982a). Measurements are given in Table 1.

Compared to those of *Grus antigone,* which weighs c. 8 kg, the leg bones of *G. melitensis* are the same size or larger. However, the syntype coracoid (BMNHL 49365) and a distal humerus (BMNHL A5162), attributed to *G. melitensis* by Harrison (1979), are smaller, which led him to the conclusion that the crane had reduced flight. These two bones actually belong to *G. grus,* so no evidence pertains to the flight capabilities of *G. melitensis,* the latter being represented chiefly by leg bones (Northcote, 1984).

The femur of *Grus melitensis* differs from that of *G. antigone* in being more robust, in lacking a well-marked ridge below the facies articularis antitrochanterica, and in having a smaller angle between the latter area and the head (Northcote, 1982a). The fossil femur also differs from that of *G. antigone* in having a well-defined fovea tendineus m. tibialis and lig. collaterale laterale (Northcote and Mourer-Chauviré, 1988). The distal tibiotarsi of *G. melitensis* and *G. antigone* are the same size, but, in the latter, the condyles are parallel to one another, whereas in *G. melitensis* the condylus medialis is directed mediad, away from the condylus lateralis (Northcote, 1984; Northcote and Mourer-Chauviré, 1985, 1988). Proximally, the tarsometatarsus of *G. melitensis* is the same width as that of *G. antigone,* but it has a larger eminentia intercondylaris that is not so clearly demarcated from the area intercondylaris (Northcote, 1982b, 1984). Distally, the tarsometatarsus of *G. melitensis* is wider mediolaterally than that of *G. antigone.* The trochleae are more splayed (Northcote, 1982a). The proximal phalanx of the second pedal digit of *G. melitensis* differs from that of *G. antigone* in having a rounder, better-defined medial fovea ligamenta collateralis (Northcote and Mourer-Chauviré, 1988). The phalanx is also shorter and stouter than in *G. antigone.* Thus, the hindlimb bones of *G. melitensis* can be distinguished from those of *G. antigone.* They can also be distinguished from those of the similarly sized extinct crane *G. primigenia* from Europe (Northcote and Mourer-Chauviré, 1988).

The greater robustness of the femur and the more clearly marked areas for tibial tendon and ligament attachment distally in *Grus melitensis* may indicate greater strength, in comparison with *G. antigone,* especially at the knee joint. In *G. melitensis,* the more proximal direction of the femur head may have maintained the legs closer to the midline than in *G. antigone.* The greater splaying of the tibiotarsal condyles, for accommodation of the larger eminentia intercondylaris of the tarsometatarsus,

and the greater splaying of the tarsometatarsal trochleae, for spreading the shorter, stouter toes, would have contributed to more stable foot movement in *G. melitensis*. All these features suggest that, compared to *G. antigone*, *G. melitensis* walked more efficiently.

Grus grus (Linnaeus 1758)

Crane

Specimens of *Grus grus* comprise the coracoid from Zebbug and the distal humerus from Tal Gnien that were reassigned from *G. melitensis*, another distal humerus (NMNHM Q/147) from Ghar Dalam, and a number of fossils from Mnajdra (UMZC 252a) (Northcote, 1984). The bones are the size of those of Recent *G. grus*. Flocks of *G. grus* migrate over Sicily and Malta (Zammit, 1981–1983), but they evidently lived there in the last interglacial. In the last glacial, *G. grus* was widespread in Europe (Brodkorb, 1967).

DISCUSSION

HABITAT

Humidity and temperature were probably higher on Malta at times during the last interglacial than now (Van der Hammen et al., 1971). Remains of pygmy elephants and hippopotami, giant dormice, land and freshwater turtles (Adams, 1870, 1877), geese (Parker, 1865, 1869; Bate, 1916), and the swans and cranes discussed here have been found. They indicate that about 125,000 yr ago the island had lush vegetation, abundant fresh water and marshland, fen carr, and forest. Trees, ferns, and herbs were abundant (Suc, 1984; Turon, 1984). Parker (1865, 1869) and Bate (1916) thought foxes preyed on the fauna. However, Falconer (1868:appendix) and Adams (1870:167) noted the absence of carnivore bones from their Maltese excavations. Sondaar and Boekschoten (1967) and Sondaar (1971) expressed the opinion that no large predators existed on Mediterranean islands during this interglacial. Zammit-Maempel (1982) recorded Pleistocene bear remains on Malta but noted their rarity.

The different morphology of *Cygnus falconeri*, *C. equitum*, and *C. c. cygnus* adapted these swans to different types of terrestrial behavior (Northcote, 1988). The same may be said in comparing *Grus melitensis* with *G. grus* and *G. antigone*. The latter two both eat land and aquatic plants but usually breed in wetlands (Cramp and Simmons, 1980). *Grus melitensis* may have been more terrestrial than *G. grus* or *G. antigone*.

EVOLUTION

Cygnus falconeri and *C. equitum* presumably came from the flighted Eurasian stock that, according to Johnsgard (1974), produced *C. cygnus*. Terrestrial anseriforms are considered to be more specialized than aquatic anseriforms (Johnsgard, 1965; Olson and Feduccia, 1980); hence, *C. c. cygnus* is considered to be more specialized than *C. olor*. *Cygnus falconeri* and *C. equitum*, being even more terrestrial, may have been more specialized than *C. c. cygnus*. Fossils of *C. falconeri* are chiefly of hindlimbs, whereas those of *C. equitum* are chiefly of forelimbs. This precludes an accurate hypothesis of their relationships. *Grus melitensis*, represented chiefly by hindlimb bones, presents a similar problem. An account of *G. primigenia* (in prep.) may indicate the relationships of the European cranes. No remains of *C. falconeri*, *C. equitum*, or *G. melitensis* have ever been found outside the Mediterranean islands. They probably evolved via allopatric speciation from separate invasions of ancestors derived from Europe (Northcote, 1988). At the end of the last interglacial on Malta, falling temperatures and tectonic disturbance resulted in sea-level changes and tilting and erosion of the land. This caused the disappearance of the rich island habitats (Northcote, 1988). The less specialized, migratory *C. c. cygnus* and *G. grus* survived the loss of these island habitats, but *C. falconeri*, *C. equitum*, and *G. melitensis* may have become too specialized and dependent on the island habitats to adapt to the changing conditions. This may have led to their extinction.

SUMMARY

Swans, two extinct and one extant species, and cranes, one extinct and one extant species, are described from the last interglacial (c. 125,000 B.P.) of Malta. Scaling formulae are used for estimating the weight and wingspan of the extinct swans. The fossils of *Cygnus falconeri* are closer to *C. cygnus* than to *C. olor* in general structure and there is no frontal knob. However, the femur and tarsometatarsus are stouter than in *C. cygnus cygnus*, and the toe bones are shorter and stouter than in Recent swans. *Cygnus falconeri* had a small glandulae nasalis, suggesting that it did not feed near salt water. It was probably an efficient walker and habitually foraged on land. *Cygnus falconeri* weighed c. 17 kg and had a wingspan of c. 3 m. It was larger and had more limited flight capability than other Palaearctic swans. *Cygnus equitum* is undoubtedly a swan, but, compared to Recent Palaearctic swans, it had longer coracoids that indicate a broader body, deeper sulci for the parts of the triceps muscle, and stouter bones. Except for the relative shortness of the distal wing bones, *C. equitum* is closer to *C. cygnus* than to *C. olor* in general structure and there is no frontal knob. The stouter shape of the vertebrae, the presence of an impressio m. supracoracoidei on the humerus, the flaring of the lateral condyle of the femur, and the form of a trochlear groove are goose-like characters. *Cygnus equitum* weighed c. 3.5 kg and had a wingspan of 1.20–1.78 m. It is the smallest known swan. Its wings were feathered and its flight apparatus was not reduced, so no evidence indicates that it was flightless. *Cygnus equitum* could feed near fresh and salt water, as indicated by the large glandulae nasalis; it walked efficiently and may have taken off and landed on level ground. Its wing skeleton and small, broad body suggest that *C. equitum* may have lived, fairly sedentarily, in enclosed habitats. *Cygnus c. cygnus*, now occurring only accidentally in the western Mediterranean, used to live on Malta. *Cygnus falconeri* and *C. equitum* probably came from the same ancestral stock as *C. c. cygnus*, but they were more terrestrial and specialized.

Grus melitensis was similar in size to *G. antigone*, which weighs c. 8 kg, but differs morphologically from it and the extinct *G. primigenia* from Europe. Compared to *G. antigone*, *G. melitensis* had a more robust femur, legs held more closely to the midline by a more proximally directed femoral head, and a firmer knee joint indicated by the more clearly marked areas for the tibial tendons and the lateral ligaments. It also had a more efficient craniocaudal foot movement as a result of the splaying of the tibiotarsal condyles to accommodate the larger eminentia intercondylaris of the tarsometatarsus. In addition, there was a more stable foot, with perhaps shorter, stouter, and more splayed toes. All these factors suggest that *G. melitensis* walked more efficiently and was more terrestrial than *G. antigone* and *G. grus*, which have similar habits. Both the small syntype coracoid and a small humerus that Harrison (1979) attributed to *G. melitensis* belong to *G. grus*, thereby refuting the hypothesis that the extinct crane had small wings and reduced flight. At this point, no assessment of the phylogenetic relationships or body form of

G. melitensis is possible. *Grus grus*, now only migratory over the Maltese islands, used to live on Malta.

A warm moist climate, a scarcity of predators, isolation, and an abundance of lush vegetation, fresh water, marshland, and woodland facilitated specialization on Malta. At the end of the last interglacial, the climatically induced loss of habitats led to the failure of *Cygnus c. cygnus* and *Grus grus* to return to the island and caused *C. falconeri*, *C. equitum*, and *G. melitensis* to become extinct.

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PALEOLITHIC BIRDS OF THE CRIMEAN PENINSULA, USSR

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ABSTRACT. The Paleolithic avifauna of the Crimea was investigated using bird bone remains from the grottos Prolom 2 and Zaskalnayas V and VI, as well as remains from the Chokurcha, Adzhi-Koba, and Syuren 1 caves. The Middle Paleolithic (Moustierian) avifauna included 35 species and the Late Paleolithic avifauna included 93 species. An analysis of the changes in the avifauna of the Crimean Peninsula during the Paleolithic is presented, as a result of which two climatic phases of the Moustierian can be tentatively distinguished. The relationship of the Crimean avifaunas to the late Pleistocene avifaunas of southern Europe and the Caucasus is discussed.

Key words: Paleolithic, Crimean Peninsula, USSR, Aves.

INTRODUCTION

A general knowledge of the history of the avifauna of the Crimean Peninsula is based on bird bone remains recovered in the course of archeological excavations of karst caves and shelters that had been inhabited by Paleolithic man. The first investigations of late Pleistocene birds by Tugarinov (1937) and Voinstvenskii (1963, 1967) showed that the avifauna of the Crimea represented a combination of species widely distributed in the Mediterranean region at the end of the Würm glacial phase, rather than those living in the Crimea today. These scientists were the first to distinguish arctic and alpine species in the late Pleistocene avifauna of the Crimean Peninsula that had disappeared from the region by the end of the Mesolithic epoch.

The early studies of fossil bird assemblages of the Crimea were based on the extensive, but only tentatively identified, specimens from Late Paleolithic (Syuren 1, Adzhi-Koba) and postglacial (Syuren 2, Alimovskii Naves, etc.) sites, and on less representative collections from the Middle Paleolithic (Moustierian) sites of Kiik-Koba, Shaitan-Koba, Adzhi-Koba, and Staroselye (Fig. 1). The principal conclusions concerning the landscape and climatic environments of the Crimean Peninsula were based on the composition of the avian species assemblages of these sites as a whole, without dividing them into time horizons. A total of 102 species was identified in the Paleolithic avifauna of the Crimea (Voinstvenskii, 1967).

New material obtained from the excavations of the Moustierian sites Prolom 2 and Zaskalnayas V and VI (collected by Yu. G. Kolosov in 1982, 1983, and 1985), along with the examination of the collections in the Zoological Institute of the Academy of Sciences of the USSR in Leningrad and related published data, allows a more detailed characterization of the Paleolithic and Mesolithic avifaunas of the Crimea.

MATERIAL AND METHODS

We have identified avian remains from the Prolom 2 (excavated in 1982 and 1985), Zaskalnaya V, and Zaskalnaya VI (excavated in 1985) sites and have also studied materials from Adzhi-Koba, Chokurcha, and Syuren 1 housed in the Zoological Institute of the Academy of Sciences of the USSR in Leningrad. These latter materials had been identified earlier and some of the data were published by Tugarinov (1937) and Voinstvenskii (1967). All collections from the Moustierian deposits were examined and, when necessary, identifications were corrected. Previous identifications of Late Paleolithic fossils required only minor taxonomic changes. A total of 647 fossil bird bones were studied, of which 565 were identified to species and 61 to genus only.

The Recent distribution and the character of the extant species in the Crimea are based on the data of Kostin (1983). The systematics follows that of Howard and Moor (1984).

SITE DESCRIPTIONS

Thus far, remains of birds have been found at 12 Paleolithic sites. Those with reliable archeological dating of cultural strata are located mainly along the northern foothills of the Peninsula.

MOUSTIERIAN

Staroselye

This site is located in a rock shelter on the eastern outskirts of Bakchisarai, on the left bank of the Kuchuksu stream, which flows into the Kacha River. The site was found and excavated by A.A. Formosov in 1953–1956. The bird remains were associated with the upper part of a Moustierian bed. Voinstvenskii (1967) identified three species from this site (Table 1).

Shaitan-Koba

Located on the right side of the Bodrak River valley between Simferopol and Bakchisarai, this site was investigated by G.A. Bonch-Osmolovski in 1929–1930. The remains of six species of

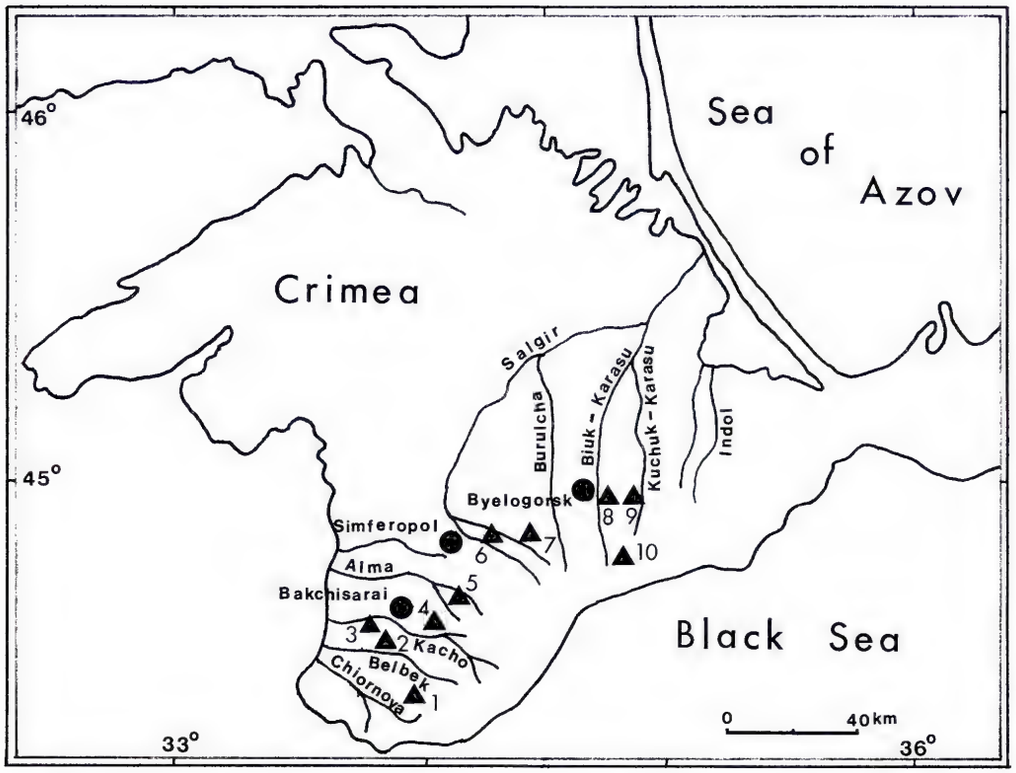

Figure 1. Map showing Paleolithic sites of the Crimea discussed in text. **1,** Fatma-Koba; **2,** Syuren 1 and 2; **3,** Alimovskii Naves; **4,** Staroselye; **5,** Shaitan-Koba; **6,** Chokurcha; **7,** Kiik-Koba; **8,** Zaskalnayas V and VI; **9,** Prolom 2; **10,** Adzhi-Koba.

birds (Table 1) were found in a bed of yellow rock waste that was not divided into different horizons. The species represented were characteristic of forest habitat.

Chokurcha

This cave is in the valley of the Malyi Salgir River, 2 km northeast of Simferopol. It was excavated under the guidance of N.L. Ernst in 1930–1940. The loose deposits were 4 m thick. Four cultural strata were distinguished, the oldest three (Nos. 2–4) of which were dated to the Moustierian epoch. The six species of birds identified from this site (Table 1) suggest open habitats. Of special interest was the recovery of an element of the Snowy Owl, *Nyctea scandiaca* (Linnaeus 1758).

Kiik-Koba

This cave is located on the right bank of the Zuia River near the village of Lesnoye, Zuisk District, 25 km east of Simferopol. It was investigated by Bonch-Osmolovski in 1924–1926. Within the cave, it was possible to distinguish earlier Moustierian strata (Nos. 4–6) and upper Holocene Tardenois strata (Nos. 1, 2). The bird remains were identified by A.Ya. Tugarinov and M.A. Voinstvenskii. In the Moustierian deposits, remains of 11 species occurred (Table 1), with a majority indicative of forest habitat.

Zaskalnayas

The group of sites Zaskalnaya V, Zaskalnaya VI, and others are located on the right side of Krasnaya Balka (Red Ravine) in the valley of the Biuk-Karasu River, 7 km north of Byelogorsk. The first two sites had in ancient times been located in large caves whose roofs later collapsed. The level of Zaskalnaya VI is 60 m above the thalweg of the valley. The sites were discovered and excavated by Yu.G. Kolosov in 1970–1981. At Zaskalnaya V, the loose deposits are almost 5 m thick, and eight Moustierian strata could be distinguished. In Stratum 4, the remains of *Delichon urbica* (Linnaeus 1758) (one specimen) and indeterminate passeriforms (two specimens) were found. One bone of *Aquila chrysaetus* (Linnaeus 1758) was previously reported from Stratum 4 (Kolosov, 1983). The Zaskalnaya VI site is located adjacent to the preceding one, and at this site five Moustierian strata were distinguished within a thickness of 3 m. A single small bone of *Lullula arborea* (Linnaeus 1758) was found in Stratum 2.

Prolom 2

This site is located on the left bank of the Kuchuk-Karasu River adjacent to the village of Prolom, Byelogorsk District. It is at the foot of a limestone fault ledge in a semicircular niche that, in ancient times, had a rock roof. It is 22 m above the river level. Light brown strata are 2 m thick and include in their horizons two large blocks of fallen rock (Kolosov, 1986). It was possible to distinguish four cultural strata of the Moustierian epoch. The site was discovered by Yu.G. Kolosov in 1973 and investigated in 1981–1985. Remains of birds, identified by the authors, represented 16 species (Table 2). In the upper strata (1–2) the majority of species identified from numerous remains are typically forest inhabitants. In Strata 3 and 4 the species represented are typical of open prairies. In Stratum 2, the presence of *Nyctea scandiaca* should be noted. Associated with the Snowy Owl were the remains of *Tadorna tadorna* (Linnaeus 1758),

Table 1. List of avian species and numbers of bone remains from Crimean Mousterian caves. + indicates the presence of species (the number of fossil remains is unknown).

Species	Staroselye	Shaitan-Koba	Chokurcha			Kiik-Koba
	After Voinstvenskii, 1967	Coll. Zool. Inst. Acad. Sci., USSR	After Voinstvenskii, 1967	After Vereshchagin and Baryshnikov, 1980	Coll. Zool. Inst. Acad. Sci., USSR	After Tugarinov, 1937; Voinstvenskii, 1967
Falco tinnunculus	14	1	1			1
F. cherrug	1					
Perdix perdix						1
Gallus sp.						1
Scolopax rusticola						2
Columba livia	21	1	1			1
Nyctea scandiaca					1	
Apus apus		1				+
A. melba		2				
Alauda arvensis			1			
Alauda sp.				14		
Hirundo rustica					1	
Oenanthe oenanthe						1
Turdus merula						3
T. philomelos			1			1
Garrulus glandarius			+			
Pica pica		2				
Pyrrhocorax pyrrhocorax						1
P. graculus						+
Corvus monedula		1			1	
Passeriformes indet.				8		
Aves indet.				1	1	

Ecological groups	n	%	n	%	n	%	n	%
Marsh	—	—	—	—	—	—	2	16.7
Prairie	14	38.9	1	12.5	16	72.7	3	25.0
Forest	—	—	3	37.5	1	4.6	5	41.7
Rocky	22	61.1	3	37.5	2	9.1	2	16.6
Tundra	—	—	—	—	1	4.6	—	—
Generalists	—	—	1	12.5	2	9.1	+	+
Total	36		8		22		12	

Perdix perdix (Linnaeus 1758), and several species of corvids (39 percent of the total specimens), possibly prey of the large owl.

Adzhi-Koba

This is a multistratified cave site on the western slope of Karabi-Yaila, approximately 15 km south of Byelogorsk. Excavations were carried out by G.A. Bonch-Osmolovski in 1932–1933. Cave deposits there include Moustierian (Nos. 3, 4) and Upper Paleolithic (No. 2) strata. Numerous bird remains from this site were identified by Tugarinov (1937) and Voinstvenskii (1967). We have introduced a few more details and supplemented the identifications, so the collection now contains 59 species (Table 3). Strata 3 and 4 are characterized by birds of prairie and rocky habitats. The Upper Paleolithic stratum also contains the remains of predominantly open landscape inhabitants. However, a considerable number of the remains were those of forest species, especially in the upper part of the stratum. Special mention should be made of the find in Stratum 2 of two northern species, *Lagopus lagopus* (Linnaeus 1758) and *L. mutus* (Montin 1776). *Perdix perdix* predominates at all levels (59 percent of the total number of specimens). Remains of crows (*Corvus* spp.) constituted 18.5 percent of the total collection.

LATE PALEOLITHIC

Syuren 1

The Syuren 1 cave is located on the right bank of the Belbek River, 13 km southwest of Bakchisarai. Excavations were conducted by G.A. Bonch-Osmolovski in 1926–1929. Three cultural strata of the Upper Paleolithic (Nos. 2–4) were distinguished in a 4-m-thick mass of deposits. The avian remains were

Table 2. List of avian species and numbers of fossil bones from each stratum of the grotto Prolom 2.

Species	Stratum 4	Stratum 3				Stratum 2	Strata 1–2	Stratum 1	Strata 1–4
		4	3	2	1				
Tadorna ferruginea	1					1			
Falco tinnunculus	2								
F. vespertinus								1	
Perdix perdix					2	3			1
Columba livia				1					
C. palumbus	1				1				
C. sp.						1			
Nyctea scandiaca						1			
Lullula arborea							1		
Alauda arvensis								1	
Erithacus sp.						1			
Chloris chloris						1			
Pica pica				1		2			
Corvus monedula		1	1		1	3			
C. frugilegus			1	1					
C. corax	1					1			
Passeriformes indet.	3					4	3	3	
Aves indet.						4	2		

Ecological groups	n	%	n	%
Marsh	1	6.2	1	5.9
Prairie	5	31.2	4	23.5
Forest	3	18.7	6	35.3
Rocky	1	6.2	1	5.9
Tundra	—	—	1	5.9
Generalists	6	37.7	4	23.5
Total	16		17	

Table 3. List of avian species and numbers of fossil bones from the cave Adzhi-Koba. + indicates the presence of species (the number of fossil remains is unknown).

Species	Coll. Zoological Institute, Academy of Sciences, USSR													After Voinstvenskii, 1967
	Moustierian								Upper Paleolithic					
	Stratum 4	Stratum 3					Stratum 3?	Strata 2–3	Stratum 2					
		5	4	3	2	2–5			4	3	2	1	1–4	
Podiceps auritus													1	
P. nigricollis								1						2
Anas penelope													2	
A. platyrhynchos							1							
A. acuta												1		+
A. querquedula														2
Aythia nyroca					1							2	1	
A. fuligula												1		3
Bucephala clangula													1	1
Mergus serrator											1			1
M. merganser											1			
Circus pygargus											1			
Falco naumanni										1				
F. tinnunculus								1			3		1	
F. vespertinus			1								1			
F. cherrug														1
Lagopus mutus								4						8

Table 3. Continued.

Species	Coll. Zoological Institute, Academy of Sciences, USSR													After Voinstvenskii, 1967
	Moustierian								Upper Paleolithic					
	Stratum 4	Stratum 3					Stratum 3?	Strata 2–3	Stratum 2					
		5	4	3	2	2–5			4	3	2	1	1–4	
L. lagopus								6				3		2
Lyrurus tetrix								1				2		
Perdix perdix	1	1	1	7	15	2	14	73	22	12	55	118	31	1
Coturnix coturnix								1		1	3	3		5
Crex crex								1						
Porzana porzana								1			1			
Gallinula chloropus														1
Vanellus vanellus												1		
Charadrius alexandrinus (?)														1
Tringa totanus														1
T. ochropus														2
T. glareola											1			
Actitis hypoleucos											1	1	1	
Philomachus pugnax													1	
Scolopax rusticola											1			
Columba livia					2						1			
Surnia ulula												1		
Strix aluco							1							1
Asio flammeus									1	1				
Melanocorypha calandra							1	3			2	3	1	
M. yeltoniensis					1		1	2						
Galerida cristata				1			1			4	2	1	2	
Lullula arborea														1
Alauda arvensis								1						
Eremophila alpestris														2
Anthus campestris														1
Prunella modularis														1
Oenanthe oenanthe														1
Turdus merula											5	3	2	
T. pilaris								2						
T. philomelos						1		4	1	1	7	13	6	
Emberiza calandra														2
Chloris chloris														1
Carduelis carduelis														+
Coccothraustes coccothraustes										1				3
Passer montanus														1
Sturnus vulgaris												1	2	
Garrulus glandarius								1				1		
Pica pica								6				5		
Pyrrhocorax pyrrhocorax								2	1	1	2	3		5
P. graculus					5		1	11	2	2	8	10	2	
P. pyrrhocorax or *P. graculus*	1	1			2		1	2	3	1	5	10	1	
Corvus monedula								3	1	2	2	9	4	

Ecological groups	n	%	n	%
Marsh	19	3.5	2	3.1
Prairie	348	64.8	46	71.9
Forest	68	12.7	3	4.7
Rocky	67	12.5	13	20.3
Tundra	14	2.6	—	—
Generalists	21	3.9	—	—
Total	537		64	

Table 4. List of avian species and numbers of bone remains from the grotto Syuren 1. + indicates the presence of species (the number of fossil remains is unknown).

	Coll. Zool. Inst. Acad. Sci., USSR				After Tugarinov, 1937; Voinstvenskii, 1967			
	Strata				Strata			
Species	4	3	2	2–4	4	3	2	2–4
Tadorna tadorna		1				1		
Anas crecca					1			
A. platyrhynchos	1				1			
A. clypeata			1		1			
Aythia nyroca	1				+			
Circus cyaneus	1				1			
C. pygargus					1			
Accipiter nisus					1			
Buteo lagopus(?)	1				1			
Aquila chrysaetus	2				2			
Falco naumanni(?)	2				2			
F. tinnunculus	8	2	1	2	+	+	+	
F. vespertinus	2		2	1	+		+	5
F. columbarius	1				1			
F. subbuteo					1			
Lagopus lagopus	4	2			+	+		6
Lyrurus tetrix	32	5	2	3	+	+	+	
Perdix perdix	25	1	4		+	+	+	
Coturnix coturnix					1			
Phasianus colchicus	1						2	
Crex crex	1	1	1	1	1	1	1	1
Porzana porzana	2				2			
Tetrax tetrax							1	
Vanellus vanellus					1			
Tringa ochropus			1				1	
Scolopax rusticola					1		1	
Chlidonias nigra					1			
Columba livia	24	3	8	4	+	+	+	
C. palumbus	1				1			
Streptopelia turtur					1			
Otus scops	1				1			
Athene noctua			1				1	
Asio otus			1				1	
Aegolius funereus								1
Apus apus	3				+			
Picoides medius							1	
P. major			1					+
Melanocorypha calandra								1
M. yeltoniensis	2			2		+		
Galerida cristata	2			1		+		
Lullula arborea								2
Alauda arvensis	4			2		+		
Eremophila alpestris	2		2			+		
Hirundo rustica	1		1	1	+		+	3
Anthus campestris								1
A. trivialis								5
Lanius cristatus								1
Prunella modularis								1
Erithacus rubecula								9
Saxicola rubetra								1
Oenanthe oenanthe	2				1		1	
Turdus morula					3			
T. pilaris	2				+			
T. philomelos					1			
Parus major								4
Emberiza calandra					3			

Table 4. Continued.

Species	Coll. Zool. Inst. Acad. Sci., USSR				After Tugarinov, 1937; Voinstvenskii, 1967			
	Strata				Strata			
	4	3	2	2–4	4	3	2	2–4
E. hortulana	2					2		
Plectophenax nivalis	1		3			1	1	
Chloris chloris								2
Carduelis carduelis								1
Loxia curvirostra	2		1	2		+		
Coccothraustes coccothraustes							4	
Passer domesticus								4
P. montanus								2
Petronia petronia							18	
Montifringilla nivalis							29	
Sturnus vulgaris	1					1		
Garrulus glandarius					+		+	7
Pica pica	19	3	12	4	+	+	+	
Pyrrhocorax pyrrhocorax	8		32	5	+	+	+	>100
P. graculus	34	8	54	18	+	+	+	<100
P. pyrrhocorax or *P. graculus*	18	2	11	3				
Corvus monedula	29	5	12	3	+	+	+	
C. frugilegus			2					2
C. cornix	1			1	1		1	

Ecological groups	n	%
Marsh	7	1.5
Prairie	76	15.8
Forest	102	21.2
Rocky	235	48.8
Tundra	6	1.1
Generalists	56	11.6
Total	487	

identified by Tugarinov (1937) and Voinstvenskii (1967). We have detailed the distribution through the strata and the number of remains (Table 4). A total of 75 species was identified. The composition of ecological groups is approximately the same for each stratum and is characterized by a dominance of the birds of rocky and forest habitats. Most numerous are the remains of corvids (59 percent of the collection), of which 68 percent are bones of *Pyrrhocorax graculus* (Linnaeus 1766) and *P. pyrrhocorax* (Linnaeus 1758). Some bones of *Lagopus lagopus* were also present.

END OF PALEOLITHIC–MESOLITHIC

Syuren 2

Syuren 2 is a Mesolithic site in a rock shelter in the vicinity of Syuren 1. It was investigated in 1924 and 1926 by G.A. Bonch-Osmolovski and in 1954–1955 by E.A. Vekilova. The bird bones, identified by Voinstvenskii (1967), included 12 species of predominantly forest species (Table 5).

Alimovskii Naves

Alimovskii Naves, a multistratified site, with strata of the terminal Paleolithic, the Mesolithic and Neolithic, is located on the left shore of the Kacha River, about 15 km southeast of Bakchisarai. The site was excavated in 1952 by A.A. Formosov and in 1955–1956 by A.D. Stoliar. Bird bone remains from the lower strata were studied by M.A. Voinstvenskii; 32 species were from the Azil epoch and birds of open habitats predominated (Table 5). The presence of *Lagopus lagopus* is of special interest.

Fatma-Koba

The Fatma-Koba site is near the village of Peredovoye of the Kuibyshevsk District. It was investigated by G.A. Bonch-Osmolvski in 1927. Fossil bird bones were recovered from both the lower (Azil) and upper (Tardenois) strata. Voinstvenskii (1967) reported four species from the Azil deposits: *Falco vespertinus* Linnaeus 1766, *Otis tarda* Linnaeus 1758, *Passer domesticus* (Linnaeus 1758), and *Pyrrhocorax graculus*.

PALEOFAUNAL REVIEW

MOUSTIERIAN

The Moustierian avifauna of the Crimea numbered not less than 36 species of eight orders, or about 9 percent of the present species composition. We have identified 10 species that had not been noted earlier for the Moustierian epoch of the Crimea, i.e., *Tadorna ferruginea* (Pallas 1764), *Columba rupestris* Pallas 1811, *Columba palumbus* Linnaeus 1758, *Nyctea scandiaca*,

Table 5. List of avian species and numbers of bone remains from sites of the end of the Paleolithic–Mesolithic (after Voinstvenskii, 1967).

Species	Alimovskii Naves	Syuren 2
Cygnus olor or *C. cygnus*		1
Falco tinnunculus	1	
Lagopus lagopus	3	
Lyrurus tetrix	2	
Perdix perdix	29	1
Coturnix coturnix	5	
Fulica atra	1	
Himantopus himantopus	1	
Scolopax rusticola	1	
Columba livia	2	3
Otus scops	1	
Athene noctua	1	
Apus apus	3	
Coracias garrulus		1
Upupa epops		3
Motacilla alba	1	
Erithacus rubecula	1	
E. megarhynchos	1	
Phoenicurus phoenicurus	1	
Oenanthe oenanthe	1	
Turdus merula	1	3
T. philomelos		2
T. viscivoris	1	
Turdus sp.		1
Ficedula albicollis		1
Aegithalos caudatus	1	
Parus major	2	
Emberiza calandra	2	
E. citrinella	1	
E. cia	4	
Carduelis carduelis	2	
Coccothraustes coccothraustes	2	
Passer domesticus	2	
P. montanus	1	
Petronia petronia	1	
Garrulus glandarius		2
Pica pica	1	4
Pyrrhocorax pyrrhocorax		1
P. graculus	6	
Pyrrhocorax sp.		2
Corvus monedula	1	4

Ecological groups	n	%	n	%
Marsh	3	3.6	—	—
Prairie	46	55.4	5	17.9
Forest	18	21.7	13	46.4
Rocky	12	14.5	6	21.4
Tundra	3	3.6	—	—
Generalists	1	1.2	4	14.4
Total	83		28	

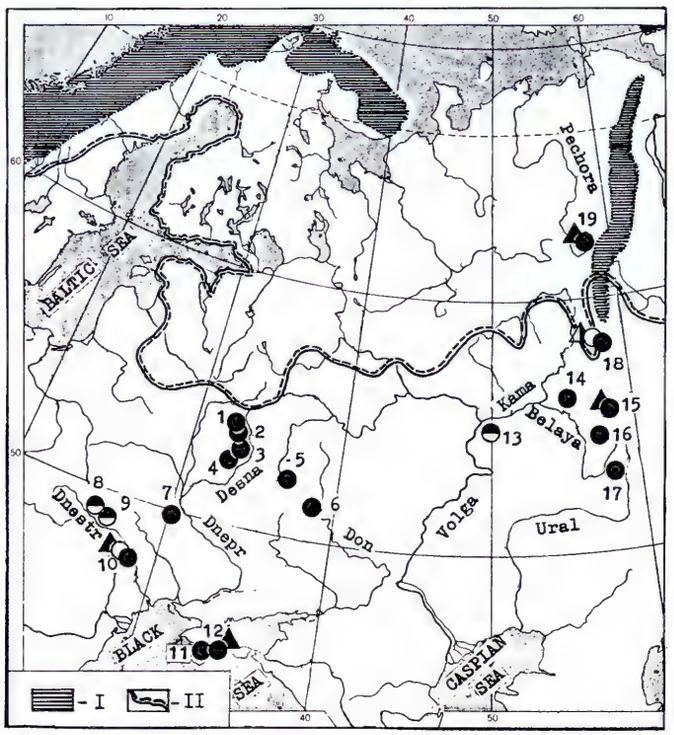

Figure 2. Map of Recent and paleodistribution of Willow Grouse (*Lagopus lagopus*) and Ptarmigan (*L. mutus*) in Eastern Europe (USSR). **I,** Recent distribution of *L. mutus;* **II,** southern boundary of Recent distributions of *L. lagopus*. Circles, *L. lagopus;* triangles, *L. mutus;* solid symbols, Late Paleolithic caves (10–12, 14–19); half-solid symbols, middle Pleistocene localities (8, 9, 13, 18); open symbols, Acheulean (10, 18) and Mousterian (10) cave layers. Localities: **1,** Hotylevo; **2,** Yeliseyevichi; **3,** Novgorod-Severskii; **4,** Mezin; **5,** Avdeyevo; **6,** Kostenki; **7,** Mezhiritch; **8,** Sinyakovo; **9,** Nizhnye Kryvche; **10,** Starye Duruitory, Buteshty; **11,** Syuren 1; **12,** Adzhi-Koba; **13,** Kharmalki; **14,** Ignatyevskaya; **15,** Klyuchevaya; **16,** Sergievskaya; **17,** Smelovskaya II; **18,** Grot Bolshoi Glukhoi; **19,** Medvezhya.

Melanocorypha yeltoniensis (Forster 1768), *Galerida cristata* (Linnaeus 1758), *Delichon urbica*, *Luscinia* sp., *Carduelis chloris* (Linnaeus 1758), and *Corvus corax* Linnaeus 1758.

Five species either do not occur on the peninsula today (*Columba rupestris, Pyrrhocorax pyrrhocorax, P. graculus, Gallus* sp.) or are rare (*Nyctea scandiaca*). The first three species belong to an avian assemblage occupying a rocky highland habitat, with the owl being a characteristic inhabitant of northern boreal and tundra landscape. Almost all of the Moustierian sites of the northern foothills of the Crimea lack species associated with marsh habitat; nearly all of the birds represented belong to open habitats (prairie and rocky environments). A relatively large number of remains of forest species, as well as marsh-dwelling birds, is characteristic only of the Adzhi-Koba site, which is indicative of the existence of a stand of forest in the Crimean "highlands."

A small number of bird specimens do not always provide sufficient evidence to establish differences in the composition of ecological groups at different periods of time. However, in the Prolom 2 cave, the lower part of the strata contained bones of species associated with open areas (Table 2), while in the upper strata the number of forest inhabitants increased. In Moustierian Stratum 1, two of the three identifiable bones belong to forest birds. In the Adzhi-Koba cave, in horizons 4 and 5 of Stratum 3, two of the four bird remains were those of open habitat species and only one was from a forest species. In horizons 2 and 3 of Stratum 3, 24 bones (70.6 percent of the total) belonged to prairie birds, there being no remains of forest species (Table

3). It seems that within the Moustierian epoch, two climatic phases can be distinguished on the basis of the fossil bird data: a more xerophylic phase [Prolom 2 (Strata 3, 4), Adzhi-Koba (Stratum 3, horizons 2, 3), Staroselye, and Chokurcha] and a more mesophylic phase [Prolom 2 (Strata 1, 2), Kiik-Koba, and Shaitan-Koba].

In reliable Moustierian strata, no remains of *Lagopus lagopus* or *L. mutus* have ever been found. These species were noted, however, at Moldavian sites of the same age (Starye Duruitory), and they are typical only in Late Paleolithic sites in the Crimea (Adzhi-Koba, Syuren 1). The Crimea was one of the southernmost regions where these boreal forms penetrated in the Pleistocene (Fig. 2). Possibly the appearance of fossil ptarmigan (*Lagopus* spp.) bones in the Late Paleolithic deposits of Crimean caves reflects the process of progressive climatic cooling and desiccation in the course of the Würm glacial phase. As a possible correlative to this, the mammals *Mammuthus primigenius* (Blumenbach 1799) and *Coelodonta antiquitatis* Blumenbach 1799 were not noted in the Late Paleolithic, presumably because habitats occupied by them had receded northward.

THE LATE PALEOLITHIC

The avifauna of the Crimea in the Late Paleolithic epoch is relatively well known; 93 species have been identified (Table 6) from the material from Adzhi-Koba and Syuren 1. Of the species listed in the Moustierian epoch, nine have not yet been recorded from the Upper Paleolithic. Except for *Gallus* sp. and *Nyctea scandiaca*, the absence of these species is somewhat surprising.

The Late Paleolithic avifauna differs from the Recent Crimean avifauna by the presence of boreal and tundra forms (*Lagopus mutus, L. lagopus*) and by the abundance of species associated with rocky and rocky-alpine landscapes [*Petronia petronia* (Linnaeus 1766), *Montifringilla nivalis* (Linnaeus 1766), *Pyrrhocorax pyrrhocorax, P. graculus*]. The hypothesis of Voinstvenskii (1963:120) that "The Crimean mountains were higher during the Pleistocene, at least in places, than they are now." was based on these finds. However, it is also possible to explain the availability in the Crimea of birds of upland tundra and alpine highland landscapes by the theory of "lowered alps." That is, with the altitudes of the Crimean range equal to the present and with a lower, relative to today, hypsometric position of the boundaries of highland landscape belts during the cold epochs of the Würm glacial period, conditions suitable for high-elevation birds could exist in the Crimea. Considerable lowering of the mountain-belt boundaries in the region of the Black Sea is evident from the discovery in the Kepshinskaya cave in the Sochi District, at an elevation of only 200–250 m above sea level, of fossil remains of the alpine zone birds *Lyrurus mlokosiewiczi* (Taczanowski 1875), *Tetraogallus caucasicus* (Pallas 1811), and *Pyrrhocorax graculus* (Burchak-Abramovich, 1974). The paleoavifauna of the Crimea also included some forest forms that disappeared in the subsequent epochs, i.e., *Phasianus colchicus* Linnaeus 1758, *Lyrurus tetrix* (Linnaeus 1758), and *Picoides medius* (Linnaeus 1758) (Voinstvenskii, 1967).

Of special interest is the dominance of *Perdix perdix* and *Pyrrhocorax graculus* in horizons 1 and 2 of Stratum 2 in the Adzhi-Koba cave and in Strata 4 and 2 at the Syuren 1 site. *Lagopus lagopus* was also found there. This possibly reflects the synchronous formation of deposits within one landscape-climatic phase. There are, however, local differences between the sites. Syuren 1 is characterized by the remains of high-mountain and rocky species (49 percent of the total) along with typically forest species (21 percent), whereas, in contrast, at the higher-elevation Adzhi-Koba site prairie species predominate in the avifauna. It is interesting to note that the occurrence at both sites of the number of bones of *Pyrrhocorax graculus* is larger than that of *P. pyrrhocorax*, by the ratios of 5:1 at Adzhi-Koba (44 specimens) and 4:1 at Syuren 1 (114 specimens). Similar numerical correlations of these species are common for many Quaternary sites of western Europe (Mourer-Chauviré, 1975). At present, *P. pyrrhocorax* is the more abundant species in the mountains of the southern Palearctic.

THE TERMINAL PALEOLITHIC–MESOLITHIC

At this time, the paleoavifauna of the Crimea retained the composition of the late Würm avifaunas; i.e., birds characteristic of open areas continued to predominate, although remains of high-mountain (*Pyrrhocorax pyrrhocorax, P. graculus*) and boreal (*Lagopus lagopus*) species also occur. *Lyrurus tetrix* was found at that time, but it later disappeared from Crimea. *Lagopus lagopus* still appears in the Mesolithic epoch (Alimovskii Naves and Syuren 2 sites); thus it is the last of the arctic and boreal species that is represented in the late Pleistocene avifauna of the Crimean Peninsula to disappear.

At the same time, there was a noted increase in the number and variety of forest species, up to 46 percent of all remains in Syuren 2. This was associated with the Holocene temperature rise and the expansion of stands of forest. This tendency is even more pronounced in the Neolithic epoch (Voinstvenskii, 1967). Thus, the time of the terminal Paleolithic and the Mesolithic was one of the last stages in the ecological evolution of the Crimean avifauna and its approach to extant modern assemblages (Tugarinov, 1937).

PALEOCLIMATIC AND ZOOGEOGRAPHICAL ASPECT

As a whole, the Paleolithic paleoavifauna of Crimea includes 115 species of 11 orders, representing more than a third of the extant avifauna of the region (Table 6). In considering the whole assemblage, mention should be made not only of the variety of species, but also of the absence of endemic ones, beginning during the Moustierian epoch at the time of development of stone industries. There is a predominance of taxa of European and Mediterranean groups, but many of the most typical representatives of the latter have not been found. Among these are the large vultures, such as *Gypaetus barbatus* (Linnaeus 1758), *Aegypius monachus* (Linnaeus 1766), *Gyps fulvus* (Hablizl 1783), and *Neophron percnopterus* (Linnaeus 1758); among the galliforms are *Alectoris graeca* (Meisner 1804) and *Tetraogallus* sp.; and among the passerines are *Turdus saxatilis* Linnaeus 1766 and *Phoenicurus ochruros* (Gmelin 1774). The presence of *Lagopus lagopus, L. mutus,* and *Nyctea scandiaca* shows that during the Würm glacial phase there was a penetration from the Russian plains of elements of a boreal fauna (Fig. 2). This was also characteristic of other mountain systems of southern Europe (Janossy, 1954, 1980; Malez and Malez-Bacic, 1974). In the Crimea, *Lagopus lagopus* occupied a minor position (Marisova, 1968; Potapova, 1986), whereas in Podolia in the Russian plain and in the northern Urals they were obviously predominant in the late Pleistocene.

The hypothesis of the existence in the Pleistocene of fairly close avifaunal ties between the Crimea and the Caucasus (Voinstvenskii, 1963) does not appear to be valid. Not a single uniquely Caucasian species [e.g., *Lyrurus mlokosiewiczi, Tetraogallus caucasicus,* which had been noted by Tugarinov (1937)] was

Table 6. List of avian species of the Paleolithic–Mesolithic of the Crimean. + indicates the presence of species. Ecological groups: M, marsh; P, prairie; F, forest; R, rocks; T, tundra; U, generalists. The character of life in the Crimea: A, sedentary; B, nesting; C, wintering, passing through, vagrant.

Species	Ecological groups	Moustierian	Late Paleolithic	End of the Paleolithic–Mesolithic	Recent
Podicipediformes					
Podiceps auritus	M		+		C
P. nigricollis	M		+		C
Anseriformes					
Tadorna ferruginea	M	+			C
T. tadorna	M		+		B
Anas penelope	M		+		C
A. crecca	M		+		C
A. platyrhynchos	M	+	+		B
A. acuta	M		+		C
A. querquedula	M		+		B
A. clypeata	M		+		C
Aythia nyroca	M	+	+		C
A. fuligula	M		+		C
Bucephala clangula	M		+		C
Mergus serrator	M		+		A
M. merganser	M		+		C
Falconiformes					
Circus cyaneus	P		+		C
C. pygargus	P		+		C
Accipiter nisus	F		+		B
Buteo lagopus(?)	P		+		C
Aquila chrysaetus	P	+	+		C
Falco naumanni(?)	P		+		B
F. tinnunculus	P	+	+	+	B
F. vespertinus	F	+	+	+	B
F. columbarius	F		+		C
F. subbuteo	F		+		C
F. cherrug	R	+			B
Galliformes					
Lagopus mutus	T		+		—
L. lagopus	T		+	+	—
Lyrurus tetrix	F		+	+	—
Perdix perdix	P	+	+		A
Coturnix coturnix	P		+	+	B
Gallus sp.	F	+			—
Phasianus colchicus	F		+		—
Gruiformes					
Crex crex	P		+		B
Porzana porzana	M		+		B
Gallinula chloropus	M		+		B
Fulica atra	M			+	B
Tetrax tetrax	P		+		B
Otis tarda	P			+	B
Himantopus himantopus	M			+	B
Vanellus vanellus	M		+		B
Charadrius alexandrinus	M		+		B
Tringa totanus	M		+		B
T. ochropus	M		+		C
T. glareola	M		+		C
Actitis hypoleucos	M		+		B
Scolopax rusticola	F	+	+	+	B
Philomachus pugnax	M		+		C
Chlidonias nigra	M		+		C

Table 6. Continued.

Species	Ecological groups	Moustierian	Late Paleolithic	End of the Paleolithic–Mesolithic	Recent
Columbiformes					
Columba livia	R	+	+	+	A
C. palumbus	F	+	+		B
Columba sp.	R	+			—
Streptopelia turtur	F		+		B
Strigiformes					
Otus scops	F		+	+	B
Nyctea scandiaca	T	+			—
Surnia ulula	F		+		C
Athene noctua	F		+	+	A
Strix aluco	F	+	+		A
Asio otus	F		+		B
A. flammeus	F		+		B
Aegolius funereus	F		+		C
Apodiformes					
Apus apus	R	+	+	+	B
A. melba	R	+			B
Coraciiformes					
Coracias garrulus	P			+	B
Upupa epops	P			+	B
Piciformes					
Picoides medius	F		+		—
P. major	F		+		A
Passeriformes					
Melanocorypha calandra	P	+	+		B
M. yeltoniensis	P	+	+		C
Galerida cristata	P	+	+		A
Lullula arborea	F	+	+		C
Alauda arvensis	P	+	+		B
Eremophila alpestris	P		+		C
Hirundo rustica	U	+	+		B
Delichon urbica	U	+			B
Motacilla alba	M			+	B
Anthus campestris	P		+		B
A. trivialis	P		+		B
Larius cristatus	F		+		B
Prunella modularis	F		+		B
Erithacus rubecula	F		+	+	A
E. luscinia	F	+			C
E. megarhynchos	F			+	B
Phoenicurus phoenicurus	F			+	B
Saxicola rubetra	F		+		C
Oenanthe oenanthe	P	+	+	+	B
Turdus merula	F	+	+	+	A
T. pilaris	F		+		C
T. philomelos	F	+	+	+	B
T. viscivoris	F			+	B
Ficedula albicollis	F			+	B?
Aegithalos caudatus	F			+	A
Parus major	F		+	+	B
Emberiza calandra	P		+	+	B
E. citrinella	F			+	B?
E. cia	P			+	A
E. hortulana	F		+		B
Plectophenax nivalis	P		+		C

Table 6. Continued.

Species	Ecological groups	Moustierian	Late Paleolithic	End of the Paleolithic–Mesolithic	Recent
Carduelis carduelis	F		+	+	A
Chloris chloris	F	+	+		A
Loxia curvirostra	F		+		A
Coccothraustes coccothraustes	F		+	+	B
Passer domesticus	P		+	+	B
P. montanus	P		+	+	B
Petronia petronia	R		+	+	—
Montifringilla nivalis	R		+		—
Sturnus vulgaris	F		+		B
Garrulus glandarius	F	+	+	+	A
Pica pica	F	+	+	+	A
Pyrrhocorax pyrrhocorax	R	+	+	+	—
P. graculus	R	+	+	+	—
Corvus monedula	U	+	+	+	A
C. frugilegus	U	+	+		B
C. cornix	U		+		A
C. corax	U	+			A

found in the Crimean deposits. The presence in the Crimean Paleolithic of birds typical of rocky habitats, e.g., *Pyrrhocorax pyrrhocorax, P. graculus, Petronia petronia,* and *Montifringilla nivalis,* tends to infer general Mediterranean ties with the peninsular fauna since all of these species occur not only in the Caucasus, but also in the mountains of southern Europe. Moreover, the finds in the Crimea of boreal and tundra forms, e.g., ptarmigan (*Lagopus* sp.), that have not been noted thus far in the Caucasian Paleolithic should be regarded as indicating greater differences in the Pleistocene avifaunas of those countries than can be observed in Recent times.

Subspecies of Crimean forest birds in common with the western Caucasus, such as *Turdus merula atterima* and *Prunella modularis obscura* (Stepanian, 1978), may be of later origin, the result of a major expansion of forests during the Atlantic optimum (hypsithermal) of the Holocene. The absence of direct connections between the avifaunas of the Crimea and the Caucasus during the Pleistocene has been emphasized more than once by zoogeographers (Pidoplichko, 1954), including the cases of zoogeographical analysis of the Recent molluscan fauna (Puzanov, 1949; Likharev, 1958). Also notable are the differences in the Pleistocene mammal faunas between the two regions [e.g., the Crimea and the Caucasus were inhabited by different forms of cave bears (*Ursus spelaeus* Rosenmüller and Heinroth 1794)]. In the Caucasus, *Coelodonta antiquitatis, Rangifer tarandus* (Linnaeus 1758), *Alopex lagopus* (Linnaeus 1758) and *Microtus* (*Stenocranius*) *gregalis* (Pallas 1778) did not occur, whereas in the Crimea *Rupicapra rupicapra* (Linnaeus 1766), *Cuon alpinus* (Pallas 1811), and species of *Myoxus* Zimmerman 1780, *Dryomys* Thomas 1906, *Prometheomys* Satunin 1901, and *Chionomys* Miller 1908 were absent.

Twelve non-migratory species disappeared from the avifauna of the Crimea during the Holocene. These included avian taxa characteristic of the tundra, the greater part of the Mediterranean rocky and rocky-alpine species and some forest species. This extirpation appears to us to be connected not only with the paleoenvironmental changes, but also primarily with the island-like isolation of the Crimean mountains. Similar tendencies are tracable in the evolution of mammal complexes (Vereshchagin and Baryshnikov, 1980).

BIRDS AND MAN IN THE PALEOLITHIC

When compared with the number of bone remains of large mammals at Moustierian epoch sites such as Chokurcha (5,126 specimens) and Staroselye (18,289 specimens) (Vereshchagin and Baryshnikov, 1980), the remains of birds taken by these people represent less than 0.01 percent of the total. In the Prolom 2 cave, eight bones of partridge and shelduck were found (23.5 percent of the remains of birds); in the Adzhi-Koba cave in Stratum 3, 41 bones of partridge (64.6 percent) as well as the remains of ducks (mallards and ferruginous ducks) were recovered. The presence of these species can be interpreted as reflecting the hunting of birds by Middle Paleolithic peoples. There is a notable predominance of gallinaceous bird remains in the Crimean sites, a characteristic of the Moustierian sites in the Caucasus as well (Baryshnikov and Cherepanov, 1985).

In the strata of the Upper Paleolithic, the number of bird bones increased sharply. In Strata 2 and 2–3 of the Adzhi-Koba cave, 311 bones of partridges have already been found (57.9 percent of the total), as well as the bones of Willow Grouse and Ptarmigan, Black Grouse, and various ducks. Among the bird remains from the Syuren 1 site, those of black grouse, partridges, and the rock dove (from Stratum 4) were numerous. An abundance of corvid remains (up to 30 percent) should be noted, possibly from birds attracted to campsites by the refuse of ancient man's activity. These species assemblages may attest to improved hunting tools and methods and an increase in the importance of hunting for birds in the paleoeconomies of the Late Paleolithic.

SUMMARY

Fossil birds from Paleolithic sites of the Crimean Peninsula have been under study for more than 50 years. As a result, the checklist of fossil birds contains 115 species, 67 of which are non-

passerines. The Paleolithic avifauna of the Crimea is characterized by tundra and Mediterranean mountain species that show closer ties with the avifauna of southern Europe then with that of the Caucasus, which lies only a short distance from the Crimea. The presence of Rock Ptarmigan, Willow Grouse, mammoth, wooly rhinoceros, and reindeer in the Crimea demonstrates the close ties with the fauna of the Russian Plain.

The Crimean Peninsula is currently inhabited by 290 species, including 177 non-passerines (except seabirds). The modern composition of this region was achieved by the early Holocene when typical tundra, some boreal, and rocky Mediterranean species disappeared from the Peninsula and the forest inhabitants increased in number.

The influence of hunting activities of early man on the mammalian fauna was great, but it affected the composition of the paleoavifauna to a lesser extent. The changes in the composition of the avifauna were linked to climatic fluctuations and the isolated position of the Crimean mountains.

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[1] Russian titles translated by the authors.—Ed.

A LATE PLEISTOCENE AVIFAUNA FROM NORTHWESTERN ALABAMA

Paul W. Parmalee

ABSTRACT. Removal of three strata of bone-bearing matrix, c. 40 cm in depth, from six 1-m² units from Bell Cave, Colbert County, Alabama, in 1984 and 1987 resulted in the recovery of 280 identifiable avian remains representing at least 32 genera and 40 species. Radiocarbon dates indicate that the accumulation of vertebrate faunal material occurred between c. 25,000 B.P. and 11,500 B.P., and the species assemblage reflects both deciduous and coniferous forest, riparian, and prairie (savanna?) habitats. Expanses of prairie in close proximity to the cave are suggested by the presence of *Tympanuchus cupido* and *Spermophilus tridecemlineatus* remains in the deposit, the first record of these species for Alabama. Although several mammalian taxa with northern affinities were represented in the cave faunal assemblage, none of the identified avian species can be considered boreal. Remains of *Bonasa umbellus* and *Ectopistes migratorius* occurred in all bone-bearing strata, and their remains were the most numerous of all avian species represented. Remains of Black-billed Magpie, *Pica pica,* from Bell Cave constitute the first record of this western bird for Alabama and, combined with its occurrence in four other late Pleistocene sites in Virginia, Tennessee, and Georgia, suggest that this species was widely distributed in the southern Appalachian Mountain region during the Wisconsinan.

Key words: Pleistocene, avifauna, Alabama, Bell Cave.

INTRODUCTION

Individuals belonging to a speleological group from the Florence–Tuscumbia area of Alabama first encountered the entrance to a cave in 1983 that was to become known as Bell Cave. This name was selected because of the resonant, bell-like tone emitted by one of the huge stalactites when it was tapped with a metal instrument. Discovery of this cave was brought to the attention of Gorden L. Bell, Jr., and James Lamb of the Red Mountain Museum (RMM), Birmingham, Alabama, who, in March 1984, explored the cave and evaluated its potential as a source of significant vertebrate fossil material. Close examination of the floor matrix revealed that the cave held large quantities of bone; the decision was made to organize a 4-week excavation, which was carried out in June and July 1984.

Bell Cave, Alabama, is located in the south bluff of the Tennessee River (Tennessee River Mile 248.2; elevation above mean sea level 145.3 m), c. 11 km west of Tuscumbia, Colbert County (Fig. 1), at 87°47′32″N, 34°43′46″W, in the southern uplands that form the southwest termination of the Appalachian Mountains. The cave is an oblong room oriented northeast–southwest; it is connected to the outside river bluff entrance (Fig. 2) by a narrow tunnel approximately 30 m in length. However, the remains of animals present in the cave floor matrix, in some instances complete individuals, probably fell or "filtered" through a former opening on top of the bluff above the cave. A large fissure at the south end of the cave running from the floor to the ceiling, and now sealed, was very possibly the primary entrance during the major periods of bone accumulation. Possible denning activities and the remains of prey taken by predators such as the black bear (*Ursus americanus* Pallas 1780) and wolf (*Canis* Linnaeus 1758), both represented in the faunal assemblage, as well as those of raptors that roosted and/or nested on top of the bluff, may have contributed to the deposit. Remains of other large mammals such as white-tailed deer (*Odocoileus virginianus* Zimmermann 1780), caribou (*Rangifer tarandus* Linnaeus 1758), tapir (*Tapirus* Brunnich 1772), and long-nosed peccary (*Mylohyus nasutus* Leidy 1869) in the deposit suggest that an opening or openings that emptied into the main cave room were large enough to accommodate animals of this size that blundered into them.

Bell Cave is approximately 12 m long by 5 m wide with a maximum ceiling height of c. 10 m. This room has served as a natural settling basin for the fissure(s) deposit, and it has an accumulation of approximately 40 cm of bone-bearing mud. Beneath a sterile clay surface layer 0–20 cm thick, the deposit is distinctly separated, for the most part, into three bone-bearing strata that appear to represent different depositional events; these rest upon sterile clay at least 70 cm thick. The basal sterile layer and the overlying, bone-bearing stratum (Stratum 4) were both subaqueously deposited. A lowering of the local water table resulted in the subsequent de-watering and consolidation of these two strata, and the onset of travertine formation. Strata 1, 2, and 3 consisted of reddish textured clays. We combined Strata 1 and 2 as Stratum 1/2 because they could be distinguished only in certain floor areas. A radiocarbon date of 11,820 +450/−500 B.P. (DIC-2929) is based on collagen from the femur of a black bear recovered between 10 and 20 cm below the surface and, thus, from either lower Stratum 1 or upper Stratum 2. A radiocarbon date of 26,500 +870/−900 B.P. (DIC-3117) was obtained on collagen from bone fragments from Stratum 3 at about 40 cm below the surface and just above the

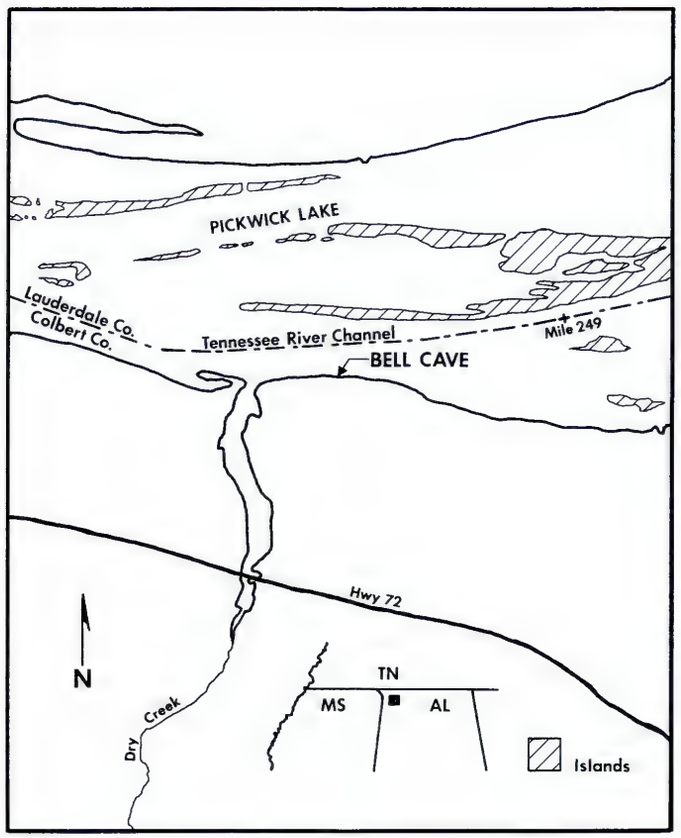

Figure 1. Map showing the approximate location of Bell Cave, Colbert County, Alabama, in relation to the Tennessee River (Pickwick Lake). Taken from U.S.G.S. 7.5 min. series topographic map, Pride Quadrangle.

Figure 2. Present entrance to Bell Cave in the north-facing bluff of the Tennessee River, mile 248.2, Colbert County, Alabama. Maximum height of entrance c. 1.5 m.

sterile layer. Stratum 3 appears to have been deposited as a viscous mudflow from the fissure, whereas Stratum 1/2 was deposited later, probably in the same manner.

The 1984 excavations took place in the southwest end of the cave where four 1-m² pits were opened (Fig. 3). The matrix from these test pits, removed one stratum at a time, was processed either at the field camp or at the RMM. The clay matrix had to be thoroughly dried before the embedded bone could be recovered. Once completely dry, the matrix would break down upon being soaked, whereupon it was hosed through a c. 17-mesh screen, leaving the remaining bones relatively clean. However, final hand brushing was necessary in many cases to remove clay residue. The collecting, drying, and washing of the matrix all resulted in unavoidable breakage, especially of bird elements. After drying, the bone was hand-picked from the screens and separated by class. Further preliminary identification work was carried out at the RMM and catalogue numbers were assigned. Each element that was tentatively identified to genus or species was given its own catalogue number, whereas the remaining bones from each pit/stratum were assigned one number.

In the hope of enlarging the avian sample, the author joined the RMM field camp for 2 days in June 1987 for the purpose of recovering matrix from at least one more pit. Although the Museum field personnel were involved in the excavation of another major Pleistocene bone deposit located near Bell Cave, they gave generously of their time and expertise, enabling the excavation of one more complete 1-m² pit (Pit #5, placed adjacent to Pit #3, which was excavated in 1984) and the removal of additional matrix from Strata 1/2 and 3 from a nearly equivalent area between Pit #5 and the cave wall. In both of these areas it was not possible to define the various strata because of a tapering of the floor toward the wall, so all fossil material from Strata 1, 2, and 3 were combined (see Table 1). These matrix samples were returned to Knoxville, Tennessee, for processing. Both the 1984 and 1987 avian bone collections are housed in the RMM paleontological collections.

SYSTEMATIC DESCRIPTIONS

The majority of avian remains recovered from late Pleistocene deposits in eastern North America are osteologically indistinguishable from those of living taxa. Identifications of the bird bones recovered from Bell Cave are based on comparisons with Recent specimens housed in the Zooarchaeology Section, Department of Anthropology, University of Tennessee, Knoxville. This collection consists of c. 430 species and 2,700 specimens; species found in eastern North America are especially well represented. A large percentage of elements were fragmented, eroded, rodent-chewed, or otherwise incomplete, making it possible to identify many bones only tentatively to species, genus, or family. The number of bones of each taxa identified from the Bell Cave avian assemblage, plus the estimated minimum number of individuals of each, is recorded by excavation unit (strata, no provenience) in Table 1.

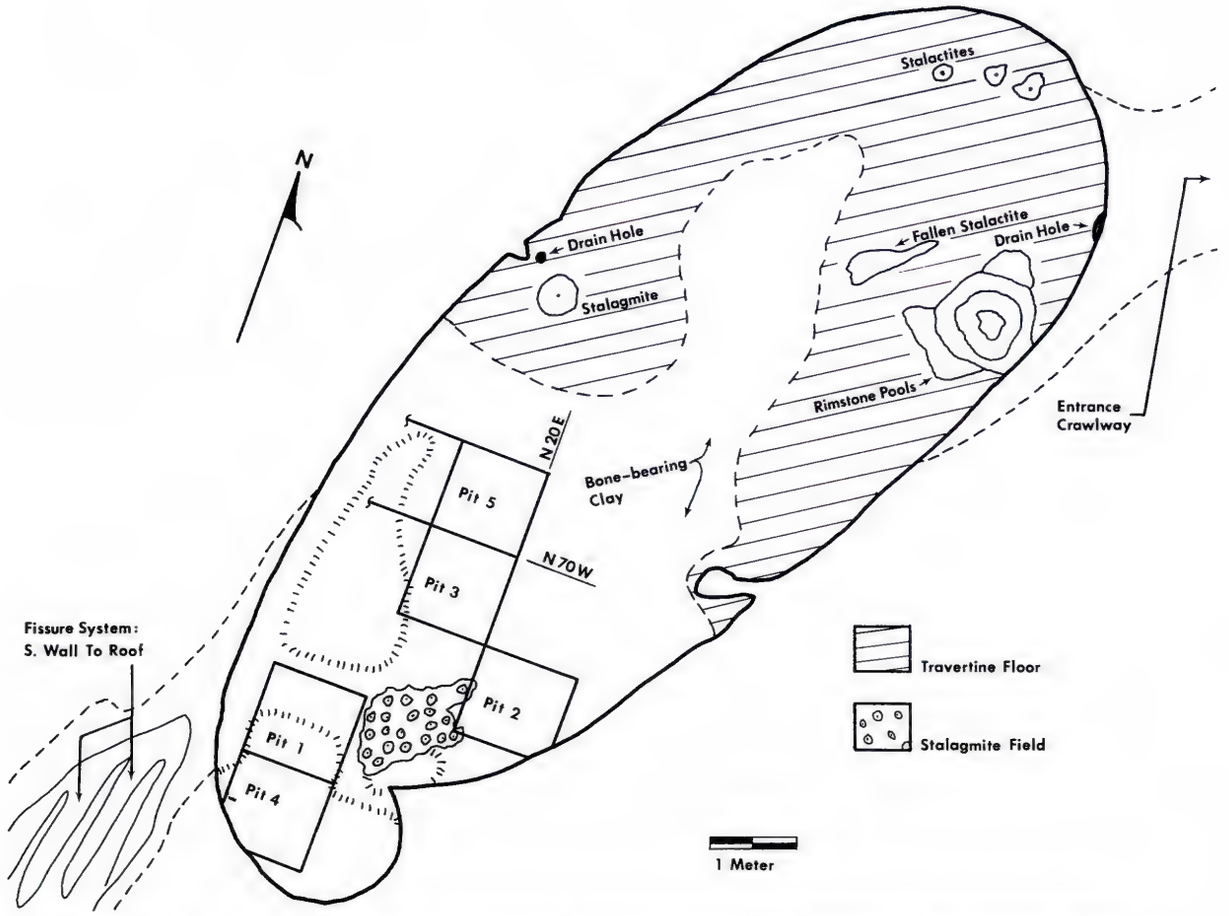

Figure 3. Scale drawing of the Bell Cave floor showing prominent geological features and placement of the excavation units.

Class Aves

Order Gaviiformes

Family Gaviidae

Genus *Gavia* Foster 1788

Gavia immer (Brunnick 1764)

Common Loon

MATERIAL. RMM 6671. Left radius, missing distal end.

REMARKS. This element was from a large, mature individual; it compares closely with the Common Loon, a fairly common migrant and an uncommon-to-rare winter resident in the Tennessee River Valley in northern Alabama.

Order Podicipediformes

Family Podicipedidae

Genus *Podilymbus* Lesson 1831

Podilymbus podiceps (Linnaeus 1758)

Pied-billed Grebe

MATERIAL. RMM 5045. Left tarsometatarsus.

REMARKS. Imhof (1962) noted that the Pied-billed Grebe is common-to-abundant on ponds and lakes throughout Alabama during the winter and that locally it may nest during the summer.

Order Anseriformes

Family Anatidae

Genus *Cygnus* Bechstein 1803

Cygnus sp. indet.

Swan

MATERIAL. RMM 6672. Cervical vertebra.

REMARKS. Although comparable in size to cervical vertebrae of the Tundra Swan, *Cygnus columbianus* (Ord 1815), this specimen from Bell Cave could not be identified to species. This swan is considered a rare transient and occasional winter resident in the state (Imhof, 1962).

Genus *Branta* Scopoli 1769

Branta canadensis (Linnaeus 1758)

Canada Goose

MATERIAL. RMM 4258, 4727, 4758, 5045, 5046–50, 6673. Sections of coracoids (3), scapula, humeri (3), carpometacarpus, tibiotarsus, synsacrum.

REMARKS. Several elements were only tentatively referred to *Branta canadensis* because of missing or rodent-chewed articular ends, but their general size and the presence of certain features, such as the line of the m. latissimus dorsi anterioris and impression of the m. brachialis anticus on humeri shafts, indicate that in all probability they were Canada Goose. Of interest was the recovery of a piece of eggshell (c. 18 × 24 mm) in Pit #4, Stratum 3. It was submitted to Lloyd F. Kiff, Western Foundation of Vertebrate Zoology, Los Angeles, California, for analysis, where, based on shell curvature and thickness, the specimen was tentatively identified as goose. The means by which the eggshell became incorporated into the deposit is a matter of speculation. Presently *B. canadensis* is a common migrant through most of Alabama and, in most years, winters in large numbers in the Tennessee River Valley.

Genus *Anas* Linnaeus 1758

Anas platyrhynchos Linnaeus 1758

Mallard

MATERIAL. RMM 3683, 3699, 4846. Right coracoids (2), distal ⅔ right tarsometatarsus.

REMARKS. Osteologically the Mallard and Black Duck, *Anas rubripes* Brewster 1902, are very similar and, as Campbell (1980: 122) has noted, "... bones of the two are extremely difficult, if not impossible, to separate." Both species are locally common to abundant fall migrants in the state and typically large numbers remain throughout the winter; some pairs remain to nest in the Tennessee River Valley.

Twelve additional duck elements were recovered in the Bell Cave matrix, but all were too fragmentary or lacked diagnostic characters so that they could not be identified to species or genus, with the exception of three referable to the genus *Anas* (RMM 4885, 4937, 5334; sternum, coracoid, tibiotarsus). The latter three were within the size range of Mallard, Pintail (*Anas acuta* Linnaeus 1758), and Gadwall (*Anas strepera* Linnaeus 1758).

Anas crecca Linnaeus 1758

Green-winged Teal

MATERIAL. RMM 5489. Left coracoid.

REMARKS. The Green-winged Teal is a common migrant and winter resident in Alabama. The shaft section of a left coracoid (RMM 5336) and right coracoid (RMM 5046), identified only as teal, may be either *Anas crecca* or the Blue-winged Teal, *A. discors* Linnaeus 1766, also a common migrant in the state.

Genus *Aythya* Boie 1822

Aythya affinis (Eyton 1838)

Lesser Scaup; or

Aythya collaris (Donovan 1809)

Ring-necked Duck

MATERIAL. RMM 5337. Sternum (partial manubrium and coracoidal sulcus).

REMARKS. Both ducks are common to abundant migrants in Alabama, and in some years they winter in considerable numbers on the Tennessee River (reservoir lakes).

Aythya sp. cf. *A. valisineria* (Wilson 1814)

Canvasback

MATERIAL. RMM 5249. Incomplete right tibiotarsus.

REMARKS. Identification of this element is tentative because both articular ends are missing. Because of its size, location of the medullary artery foramen, and length and width of the flattened fibular crest, it compared most closely with a large representative of the genus *Aythya*. The Canvasback is a regular migrant and winter resident in the Tennessee River Valley, but its yearly relative abundance varies from rare to fairly common.

Genus *Mergus* Linnaeus 1758

Mergus sp. indet.

Merganser

MATERIAL. RMM 4756, 5249, 6674. Sections of left coracoid, left femur, right ulna, synsacrum.

REMARKS. None of these elements was complete enough for species identification. Imhof (1962) notes that the Red-breasted Merganser, *Mergus serrator* Linnaeus 1758, and the Common Merganser, *Mergus merganser* Linnaeus 1758, are fairly common in the Tennessee River Valley in winter and during migration.

Order Accipitriformes

Family Accipitridae

Genus *Accipiter* Brisson 1760

Accipiter striatus Vieillot 1807

Sharp-shinned Hawk

MATERIAL. RMM 3712. Proximal half right humerus.

REMARKS. The Sharp-shinned Hawk is a locally common, permanent resident in the northern half of Alabama (Imhof, 1962).

A shaft section of a right coracoid (RMM 4937), missing the humeral articulation end, internal distal angle, and sternocoracoidal process, has been identified as that of a hawk. It compares most closely to *Buteo* Lacépède 1799, and in size to Red-shouldered Hawk, *Buteo lineatus* Gmelin 1788, but because of its fragmentary condition the genus and species remain indeterminate. A phalanx (RMM 5336) from Stratum 3 has also been identified as that of hawk, but the genus and species are indeterminate.

Genus *Haliaeetus* Savigny 1809

Haliaeetus sp. cf. *H. leucocephalus* (Linnaeus 1766)

Bald Eagle

MATERIAL. RMM 5249. Glenoid facet, coracoidal articulation, and partial neck of left scapula, missing acromion and blade.

REMARKS. Although fragmentary and rodent-chewed, this

Table 1. Avian species from late Pleistocene deposits in Bell Cave, Colbert County, Alabama, by stratigraphic unit. NP, no provenience; MNI, minimum number of individuals.

Taxon	Number of specimens in Stratum				Total		
	1/2	1/2–3	3	4	NP	Specimens	MNI
Gavia immer, Common Loon		1				1	1
Podilymbus podiceps, Pied-billed Grebe	1					1	1
Cygnus sp., swan	1					1	1
Branta canadensis, Canada Goose		3	1			4	2
cf. *B. canadensis*, Canada Goose	6					6	3
cf. *Anas platyrhynchos*, Mallard	2			1		3	1
Anas sp., duck, sp. indet.	1		1	1		3	1
Anas crecca, Green-winged Teal				1		1	1
Anas sp., teal, sp. indet.	1		1			2	1
Aythya sp. cf. *A. collaris*, Ring-necked Duck, or cf. *A. affinis*, Lesser Scaup			1			1	1
Aythya sp. cf. *A. valisineria*, Canvasback	1					1	1
Anatidae, duck, gen. et sp. indet.	5	1		1	2	9	1
Mergus sp., merganser, sp. indet.	2	2				4	1
Accipiter striatus, Sharp-shinned Hawk	1					1	1
Accipitridae, hawk, gen. et sp. indet.	1		1			2	1
cf. *Haliaeetus leucocephalus*, Bald Eagle	1					1	1
Falco sparverius, American Kestrel			1			1	1
Bonasa umbellus, Ruffed Grouse	22	6	12		2	42	7
cf. *Bonasa umbellus*, Ruffed Grouse	25	18	6		3	52	8
Tympanuchus cupido, Greater Prairie Chicken	12	5	5	1	4	27	5
Colinus virginianus, Northern Bobwhite	1	2	6			9	2
Meleagris gallopavo, Turkey	5	3	1		4	13	4
Grus sp., crane, sp. indet.					1	1	1
Philohela minor, American Woodcock	5		2	1		8	2
Bartramia longicauda, Upland Sandpiper		2	2			4	1
Catoptrophorus semipalmatus, Willet	2					2	1
Sterna sp., tern, sp. indet.			1			1	1
Ectopistes migratorius, Passenger Pigeon	16	17	13		4	50	8
Otus asio, Eastern Screech-Owl	3					3	1
cf. *Strix varia*, Barred Owl			1			1	1
cf. *Melanerpes carolinus*, Red-bellied Woodpecker		1	1			2	1
cf. *Picoides villosus*, Hairy Woodpecker	1					1	1
cf. *Sayornis phoebe*, Eastern Phoebe			1			1	1
Hirundinidae, swallow, gen. et sp. indet.	1					1	1
Cyanocitta cristata, Blue Jay	1	2	1			4	2
Pica pica, Black-billed Magpie	1	1				2	1
Corvus corax, Northern Raven	1					1	1
Dumetella carolinensis, Gray Catbird		1				1	1
Turdus migratorius, American Robin	1	1				2	1
Parulinae, wood warbler, gen. et sp. indet.	2					2	1
cf. *Piranga olivacea*, Scarlet Tanager	1					1	1
Quiscalus quiscula, Common Grackle	1		3			4	1
Passeriformes, gen. et sp. indet.	20	16	18	2		56	—
Total	144	82	79	8	20	333	75

element compares closely with *Haliaeetus leucocephalus*. In the early 1960s, the Bald Eagle was reportedly "... a locally common, breeding, winter resident on the Gulf Coast, in the Tennessee Valley, and possibly in one or two intervening places" (Imhof, 1962:187). During the past decade, however, populations of the Bald Eagle on the Tennessee River (reservoirs) in Tennessee and Alabama were restricted to wintering birds that vary in number annually from 10 to 15 individuals on each of the various reservoirs.

Family Falconidae

Genus *Falco* Linnaeus 1758

Falco sparverius Linnaeus 1758

American Kestrel

MATERIAL. RMM 4284. Distal end and metacarpal II section of left carpometacarpus.

REMARKS. This small falcon is a common, although somewhat local, permanent resident in the state, its numbers increasing considerably during the fall and winter months by an influx of birds from farther north.

Order Galliformes

Family Phasianidae

Genus *Bonasa* Stephens 1819

Bonasa umbellus (Linnaeus 1766)

Ruffed Grouse

MATERIAL. RMM 3721, 3744, 3759, 3776, 3823, 3991, 4287, 4716, 4727–9, 4738, 4756, 4886, 5043, 5046–7, 5070, 5249, 6675–6. Complete and/or sections of premaxilla, quadrates (2), humeri (15), ulna, coracoids (12), carpometacarpi (3), tarsometatarsi (6), phalanx II (2).

Bonasa sp. cf. *B. umbellus* (Linnaeus 1766)

Ruffed Grouse

MATERIAL. RMM 3749, 4727, 4738, 4756, 4886, 5046–7, 5070, 5249–51, 6675–6. Sections of premaxilla, sternum, furculum, scapulae (4), humeri (15), ulnae (3), radii (2), scapholunar, carpometacarpi (2), coracoids (15), femur, tibiotarsi (3), tarsometatarsi (3).

REMARKS. A total of 42 grouse elements were identified as Ruffed Grouse, while 52 bones, although close to those of *Bonasa umbellus* in size and structural characteristics, were either too fragmentary, eroded, rodent-chewed, or otherwise lacking in diagnostic characters to permit unequivocal species determinations. In light of the age of the deposit and representation of certain mammalian species with boreal affinities (e.g., marten, *Martes americana* Turton 1806; fisher, *Martes pennanti* Erxleben 1777), the remains of Spruce Grouse, *Dendragapus canadensis* Linnaeus 1758, at Bell Cave seemed a likely possibility. Bones of this grouse have been identified from four late Pleistocene faunal localities in Virginia (Eshelman and Grady, 1986), and Wetmore (1967) reported its occurrence at Ladds, Bartow County, Georgia, a late Pleistocene site c. 280 km ESE of Bell Cave. However, none of the grouse elements from Bell Cave could be identified as *D. canadensis,* and in all probability most if not all of the remains tentatively identified as *B. umbellus* are that species.

Imhof (1962:200) noted that "Formerly this bird [*Bonasa umbellus*] was a permanent resident in the hilly country of northeastern Alabama." Northwestern Alabama was not included as part of the bird's past distribution as shown by Aldrich and Duvall (1955). The evidence from Bell Cave, however, suggests that the Ruffed Grouse was well established and apparently common in the timbered bluffs of the Tennessee River during the late Pleistocene–early Holocene.

Genus *Tympanuchus* Gloger 1842

Tympanuchus cupido (Linnaeus 1758)

Greater Prairie Chicken

MATERIAL. RMM 3683, 3723, 3750, 3757–8, 3991, 4728, 4938, 4886, 4937, 5046–7, 5070, 5250. Complete and/or sections of humeri (12), ulnae (2), carpometacarpus, phalanx II, coracoids (6), scapulae (2), tarsometatarsi (3).

REMARKS. Remains of the Greater Prairie Chicken from Bell Cave (Fig. 4) represent the first record of this grouse from Alabama. The possibility exists, however, that some, or all, of these bones could be those of the Sharp-tailed Grouse, *Tympanuchus phasianellus* Linnaeus 1758. Wetmore (1959b:180) made the following comment relative to the osteology of these two grouse: "In detailed examination of the skeleton, element by element, beginning with the skull and continuing through sternum, pectoral girdle, wings, pelvis and posterior limb, I find that the only definite characters to separate the two groups of species appear in the pelvis. Details evident in other parts of the skeleton serve to identify species but are not valid to separate the two groups recognized as genera [*Tympanuchus, Pedioecetes*]." He identified at least four individuals of *T. phasianellus,* primarily on the basis of appendicular skeletal elements, from Natural Chimneys, Augusta County, Virginia (Wetmore, 1962). Remains of Sharp-tailed Grouse have also been reported from three other late Pleistocene sites (Back Creek Cave #1 and #2, Clark's Cave) in Bath County, Virginia (Eshelman and Grady, 1986). Elements of *T. cupido* have been found at Kingston Saltpeter Cave, Bartow County, Georgia (D.W. Steadman, pers. comm., 1988).

Remains of both *Tympanuchus phasianellus* (Pleistocene strata) and *T. cupido* (Pleistocene and lower Holocene strata) were identified from Cheek Bend Cave, a deeply stratified (c. 4.5 m) rockshelter deposit along the Duck River about 120 km NNE of Bell Cave, Maury County, Tennessee (Parmalee and Klippel, 1982). Remains of the thirteen-lined ground squirrel, *Spermophilus tridecemlineatus* Mitchell 1821, occurred at both sites in strata containing bones of *Tympanuchus,* suggesting suitable habitat (open expanses of short grass prairie and/or savanna) for Prairie Chicken and possibly Sharp-tailed Grouse. One factor affecting unequivocal species identifications of *Tympanuchus* based on osteological material is that "*T. cupido* and *T. phasianellus* hybridize sporadically, but occasionally they interbreed extensively on a local level" (American Ornithologists' Union, 1983:140).

Genus *Colinus* Goldfuss 1820

Colinus virginianus (Linnaeus 1758)

Northern Bobwhite

MATERIAL. RMM 3771, 3991, 4287, 5334, 5336, 6679. Sections of humerus, ulna, radius, carpometacarpus, scapula, sternum, coracoids (2), tarsometatarsus.

REMARKS. The Bobwhite is common over much of the state, becoming most abundant in habitat consisting of brushy fields, cutover woodlands, and fallow pastureland.

Genus *Meleagris* Linnaeus 1758

Meleagris gallopavo Linnaeus 1758

Turkey

MATERIAL. RMM 3450, 3703, 3991, 4884, 4886, 6680–1. Sections of humeri (4), radius, carpometacarpus, coracoids (2), scapula, sternum, tibiotarsus, tarsometatarsi (2).

REMARKS. Imhof (1962:202) comments that "This bird was

a common and widespread, breeding permanent resident in Alabama . . . until about 1880. It is a woodland bird and seems to thrive best on well-watered forests that are half hardwood, with a good proportion of oaks, and broken by well-dispersed clearings of native grasses, legumes, and succulent fruits."

Order Gruiformes

Family Gruidae

Genus *Grus* Pallas 1766

Grus sp. indet.

Crane

MATERIAL. RMM 6682. Fragmented and eroded proximal end of left carpometacarpus.

REMARKS. Although within the size range of Sandhill Crane, *Grus canadensis* (Linnaeus 1758), the specimen is too incomplete for species identification. Inland in Alabama, the Sandhill Crane is considered a casual transient. The Whooping Crane, *Grus americana* (Linnaeus 1758), was formerly uncommon in winter and during migration through the state (Imhof, 1962).

Order Charadriiformes

Family Scolopacidae

Genus *Philohela* Gray 1841

Philohela minor (Gmelin 1789)

American Woodcock

MATERIAL. RMM 4728, 4756, 4886, 5045, 5134, 5336. Sections of right humeri (2), left and right scapulae, right femur, right tibiotarsus, left tarsometatarsus, right coracoid.

REMARKS. An uncommon and local permanent resident in most of the state, the American Woodcock most frequently inhabits low, wet woods and swampy thickets.

Genus *Bartramia* Lesson 1831

Bartramia longicauda (Beckstein 1812)

Upland Sandpiper

MATERIAL. RMM 3991, 6683. Sections of left coracoid, right scapula, right tibiotarsi (2).

REMARKS. Imhof (1962) records the Upland Sandpiper as fairly common during migration where it frequents shortgrass fields such as hay meadows and pastures.

Genus *Catoptrophorus* Bonaparte 1827

Catoptrophorus semipalmatus (Gmelin 1789)

Willet

MATERIAL. RMM 4756, 6250. Sections of right coracoid, right scapula.

REMARKS. Although a common summer resident and uncommon winter resident along the coast, inland the Willet is uncommon-to-rare during migration. Imhof (1962) noted that it is seen most often in spring in the Tennessee Valley, where the majority of sightings have been reported from Wheeler Refuge (Tennessee River: Wheeler Reservoir), about 72 km east of Bell Cave.

Figure 4. **Top:** Left ulna (RMM 3991), internal view, and distal section of right coracoid (RMM 5046), dorsal view, of *Tympanuchus* sp. cf. *T. cupido* from Bell Cave, Alabama. Comparative specimens, outside left and right, from a Champaign County, Illinois, bird. 1.2×. **Bottom:** Left humeri (center and right, RMM 5047), anconal view, of *Tympanuchus* sp. cf. *T. cupido* from Bell Cave, Alabama. Comparative specimen, left, from Champaign County, Illinois. 1.2×.

Fragments of a distal tibiotarsus (not numbered) from a bird

the size of a Woodcock and sections of a tarsometatarsus (RMM 5337) and scapula (RMM 6684) from a small plover/sandpiper were also recovered from the cave matrix, but species determinations could not be made.

Family Laridae

Genus *Sterna* Linnaeus 1758

Sterna sp. indet.

Tern

MATERIAL. RMM 4299. Left phalanx II.

REMARKS. This element is comparable in size to those of the Common Tern, *Sterna hirundo* Linnaeus 1758, and Forster's Tern, *Sterna forsteri* Nuttall 1832, both of which are rare-to-uncommon during migration through the Tennessee River Valley, but a species determination could not be made.

Order Columbiformes

Family Columbidae

Genus *Ectopistes* Swainson 1827

Ectopistes migratorius (Linnaeus 1766)

Passenger Pigeon

MATERIAL. RMM 3762, 3771, 3991, 4287, 4727–9, 4756, 4886, 5045–7, 5070, 5250, 5335–7, 6685–6. Complete and/or sections of premaxilla, humeri (10), ulnae (5), carpometacarpi (7), phalanx II, sternum, coracoids (14), scapulae (7), tarsometatarsi (4).

REMARKS. The Passenger Pigeon wintered from Arkansas, southeastern Missouri, Tennessee, and North Carolina south to Texas, the Gulf Coast, and northern Florida (American Ornithologists' Union, 1983). There are few specific records of occurrence for this bird in Alabama, although it apparently wintered locally in considerable numbers in suitable forested regions. Schorger (1973:287) provides the following comment: "Edward Pasteur, of Greensboro [Hale County, west-central Alabama], shot one in the 'winter of 1887.' The bird was alone." This was one of the last historic records of *Ectopistes migratorius* for the state. Parmalee (1962) reported 10 elements of the Passenger Pigeon from the Stanfield–Worley Bluff Shelter, an aboriginal Archaic site (c. 9,000 B.P.) located about 13 km SW of Bell Cave. Remains of this pigeon were relatively numerous (50) in the Bell Cave avian samples, second only in numbers to Ruffed Grouse (and cf. *Bonasa umbellus*), suggesting that it was common (late fall/winter?) along the timbered bluffs of the Tennessee River during the late Pleistocene.

Order Strigiformes

Family Strigidae

Genus *Otus* Pennant 1769

Otus asio (Linnaeus 1758)

Eastern Screech-Owl

MATERIAL. RMM 3760, 3771, 4756. Sections of right coracoid, left ulna, left carpometacarpus.

REMARKS. *Otus asio* is probably the most common owl found in the state and one that typically inhabits open stands of hardwood forests, woodlots, and orchards.

Genus *Strix* Linnaeus 1758

Strix sp. cf. *S. varia* Barton 1799

Barred Owl

MATERIAL. RMM 5336. Distal end right tibiotarsus, missing the external condyle.

REMARKS. Because of its size, this fragmentary element might possibly be confused with that of a male Great Horned Owl, *Bubo virginianus* Gmelin 1788, but compared to the reference material at hand (25 specimens of *S. varia*), it is probably that of a Barred Owl. This owl is also regarded as common and widespread in Alabama, where it occurs in both dense coniferous and hardwood forests, especially those of river valleys and marshes.

Order Piciformes

Family Picidae

Genus *Melanerpes* Swainson 1832

Melanerpes sp. cf. *M. carolinus* (Linnaeus 1758)

Red-bellied Woodpecker

MATERIAL. RMM 3991, 6687. Distal end right carpometacarpus; right humerus, minus proximal end and with eroded condyles.

REMARKS. The incompleteness or eroded condition of these two elements makes species identification tentative, although both compare closely with *Melanerpes carolinus*. Imhof (1962) comments that the Red-bellied Woodpecker is a common-to-abundant permanent resident throughout the state, living in all types of woodlands.

Genus *Picoides* Lacépède 1799

Picoides sp. cf. *P. villosus* (Linnaeus 1766)

Hairy Woodpecker

MATERIAL. RMM 5251. Proximal end right tibiotarsus.

REMARKS. An inhabitant of both coniferous and deciduous woodlands, the Hairy Woodpecker is fairly common in Alabama.

Order Passeriformes

Family Tyrannidae

Genus *Sayornis* Bonaparte 1854

Sayornis sp. cf. *S. phoebe* (Latham 1790)

Eastern Phoebe

MATERIAL. RMM 3991. Proximal end right humerus.

REMARKS. "In Alabama [*Sayornis phoebe*] is a common and widely-distributed permanent resident north of the Coastal

Plain and common on migration and in winter in the rest of the state" (Imhof, 1962:349).

Family Hirundinidae
gen. et sp. indet.
Swallow

MATERIAL. RMM 5070. Shaft section of right humerus.

REMARKS. The short shaft with proportionately large diameter, wide and shallow impression of m. brachialis anticus, and large and elevated attachment of interior articular ligament are characters indicative of swallow humeri. There are six species representative of this family that occur in Alabama as permanent residents and/or migrants. This specimen was from one of the smaller species of swallows, being well below the size range of the Purple Martin, *Progne subis* Linnaeus 1758.

Family Corvidae
Genus *Cyanocitta* Strickland 1845
Cyanocitta cristata (Linnaeus 1758)
Blue Jay

MATERIAL. RMM 4286, 5336, 6688. Left humerus, proximal left humerus, distal right and left ulnae (2).

REMARKS. The Blue Jay is a common, widely distributed bird in Alabama that may be found inhabiting all types of both coniferous and hardwood forests.

Genus *Pica* Brisson 1760
Pica pica (Linnaeus 1758)
Black-billed Magpie

MATERIAL. RMM 4756, 6690. Proximal third right femur, distal end right humerus.

REMARKS. These two incomplete elements (Fig. 5) from Bell Cave compared closely with those from six specimens of Black-billed Magpie in the Department of Anthropology, The University of Tennessee osteological collections, that were obtained in Wyoming and Colorado. They represent the first record of *Pica pica* from Alabama and the fifth late Pleistocene occurrence of the species east of the Mississippi River. The other four locations include Natural Chimneys, Augusta County, Virginia (Wetmore, 1962); Strait Canyon, Highland County, Virginia (Eshelman and Grady, 1986); Baker Bluff Cave, Sullivan County, Tennessee (Guilday et al., 1978); and Kingston Saltpeter Cave, Bartow County, Georgia (D.W. Steadman, pers. comm., 1988). These five localities indicate a late Pleistocene range of this magpie in eastern North America that included the Appalachian Mountain chain southward to its most southern extension (Fig. 6). With reference to the magpie, Wetmore (1962:3) raised an interesting point: "Since I have seen the abundance of this species in much of western Europe, I have often wondered at its lack through our eastern states where wide areas seem ecologically wholly suited for it." Recovery of future avian cave deposits in this region may well substantiate the probable former widespread distribution of the magpie in eastern North America. Today it is a species tolerant of cold climates and one that occupies a variety of habitats, arid or humid, that includes savanna, shrubby grasslands, and both coniferous and hardwood forests mixed with conifers.

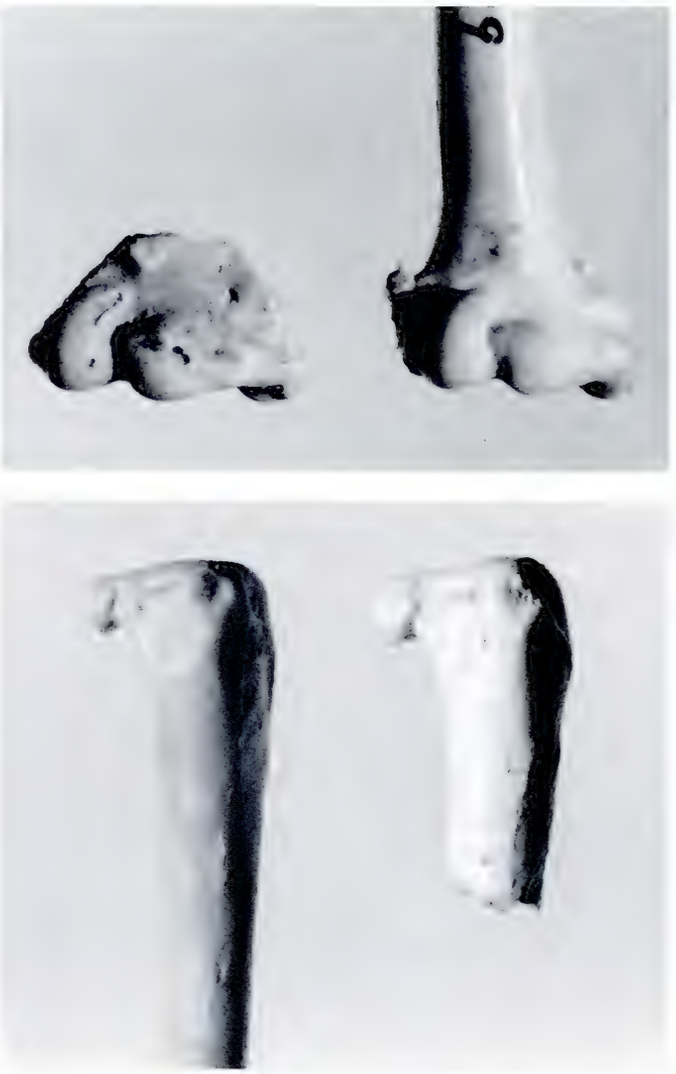

Figure 5. **Top:** Distal right humerus (left: RMM 6690) of *Pica pica*, palmar view, from Bell Cave, Alabama. Comparative specimen on right from Crook County, Wyoming. 3×. **Bottom:** Proximal third of right femur (right: RMM 4756) of *Pica pica*, posterior view, from Bell Cave, Alabama. Comparative specimen on left from Crook County, Wyoming. 3×.

Genus *Corvus* Linnaeus 1758
Corvus corax Linnaeus 1758
Common Raven

MATERIAL. RMM 3720. Right coracoid, missing sternal articulation surface.

REMARKS. Imhof (1962) stated that the Common Raven, not recorded in Alabama since 1915, was formerly a rare permanent resident in the wildest and most rugged mountain country in the northern part of the state.

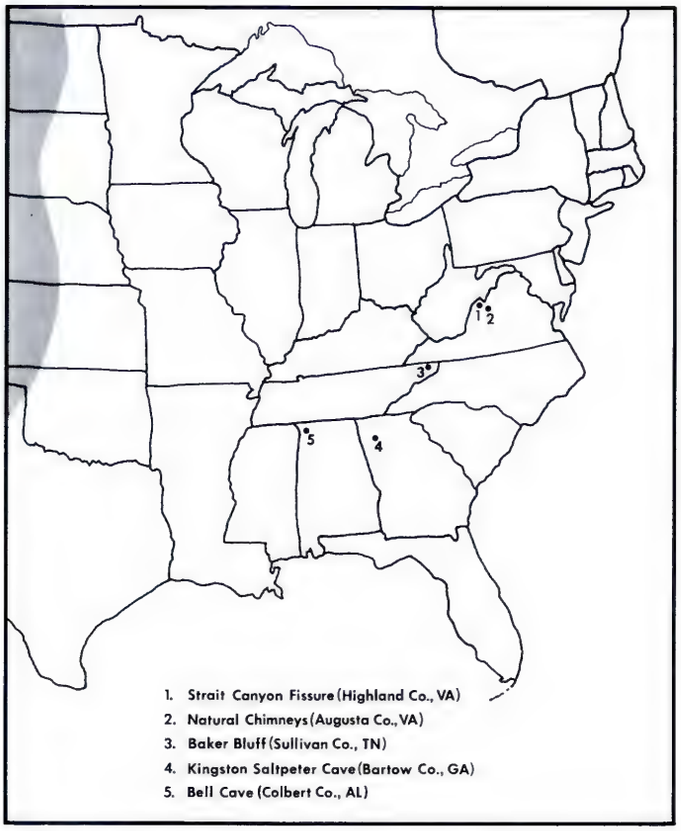
1. Strait Canyon Fissure (Highland Co., VA)
2. Natural Chimneys (Augusta Co., VA)
3. Baker Bluff (Sullivan Co., TN)
4. Kingston Saltpeter Cave (Bartow Co., GA)
5. Bell Cave (Colbert Co., AL)

Figure 6. Map of central and eastern United States illustrating the present eastern range limit of the Black-billed Magpie (shaded area) and the five late Pleistocene cave localities in the Appalachian Mountains from which remains of *Pica pica* have been recovered.

Family Mimidae

Genus *Dumetella* S.D.W. 1837

Dumetella carolinensis (Linnaeus 1766)

Gray Catbird

MATERIAL. RMM 6691. Right humerus.

REMARKS. The Gray Catbird is a common migrant throughout the state and a summer resident in most regions.

Family Muscicapidae

Subfamily Turdinae

Genus *Turdus* Linnaeus 1758

Turdus migratorius Linnaeus 1766

American Robin

MATERIAL. RMM 3756, 6689. Right humerus, left coracoid.

REMARKS. The American Robin is a common, permanent resident in Alabama above the Black Belt, a natural dry prairie region comprising c. 10,400 km^2 that extends across the south-central section of the state.

Family Emberizidae

Subfamily Parulinae gen. et sp. indet.

Warbler

MATERIAL. RMM 6692-3. Proximal end left humerus, proximal half left tarsometatarsus.

REMARKS. The proximal humerus compared most closely with *Vermivora* Swainson 1827, but a generic determination could not be made for either element.

Subfamily Thraupinae

Genus *Piranga* Vieillot 1808

Piranga sp. cf. *P. olivacea* (Gmelin 1789)

Scarlet Tanager

MATERIAL. RMM 3748. Left humerus.

REMARKS. This tanager is reported to be a common migrant through the state and "... is a locally common, breeding, summer resident, usually at higher elevations, in the Tennessee Valley and Mountain Region, ..." (Imhof, 1962:518).

Subfamily Icterinae

Genus *Quiscalus* Vieillot 1816

Quiscalus quiscula (Linnaeus 1758)

Common Grackle

MATERIAL. RMM 5020, 5336, 5338. Premaxilla, left humeri (2), humeral articulation left coracoid.

REMARKS. Although a common summer resident throughout the state, the Common Grackle becomes abundant during the winter as a result of a major influx of birds from farther north.

Order Passeriformes gen. et sp. indet.

MATERIAL. RMM 3991, 4114, 4259, 4285, 4287, 4544, 4716, 4718, 4729, 4738, 4885, 5133, 5136, 5249–50, 5334, 5336–7, 6994–5. Incomplete premaxilla, humeri (12), ulnae (6), radius, carpometacarpi (8), sternum, scapula, coracoids (13), femur, tibiotarsi (8), tarsometatarsi (4).

REMARKS. Few if any of these fragmented or otherwise incomplete passerine elements lend themselves, in my opinion, to species identification. Even when complete, many passerine bones lack diagnostic species characters. Although a few specimens were from medium-sized to large passerines, e.g., *Quiscalus* sp., the majority were from much smaller birds.

DISCUSSION

Until the recovery of the extensive bone assemblage from Bell Cave, late Pleistocene avian finds were lacking for the state of Alabama. The exhaustive compilation of avian fossil and subfossil (archaeological) records by Brodkorb (1963, 1964, 1967, 1971, 1978) in his five-part *Catalogue of Fossil Birds* contained no entries of fossil bird remains recovered in the state. None were recorded for Alabama by Lundelius et al. (1983:325), who noted

Table 2. Approximate number of species, identified bones, and minimum number of individuals (MNI) represented in the Bell Cave avifauna with generalized associated habitat type.

Habitat (species or groups)	No. of species	No. of specimens	MNI
Aquatic (loon, grebe, waterfowl, tern)	10	29	16
Riparian (willet, plover/sandpiper, crane)	3	6	3
Grassland (prairie chicken, upland sandpiper)	2	31	6
Forest (grouse, hawk, owl, pigeon, woodpecker)	8	153	28
Ecotone (turkey, quail, corvids, indet. small passerines)	11	41	17
Total	34	260	70

that "Except for the Ladds local fauna in the Piedmont of northwestern Georgia, all of the known late-Pleistocene herpetofaunal and avifaunal sites in this [southeastern] region are from the southeastern Coastal Plain or the continental shelf." Therefore, the Bell Cave avifauna is of significance because it not only serves as evidence of at least some of the species that occurred in the region during the late Wisconsinan, but also because it provides some insight into the biogeography of northwestern Alabama during the period of c. 11,500–26,000 B.P.

The varied local habitats within close proximity to the cave during this time period, as indicated by the species of birds and mammals represented in the deposit, included aquatic, riparian, forest (both coniferous and deciduous), grassland, and ecotone (Table 2). Except for the Passenger Pigeon, all avian taxa represented at Bell Cave are extant, although *Bonasa umbellus, Tympanuchus cupido, Corvus corax,* and *Pica pica* no longer occur in the region. A total of approximately 280 bones, representing at least 40 taxa, was identified to the familial, generic, or specific level. Two species, the Ruffed Grouse (permanent resident) and the Passenger Pigeon (migrant and winter resident), accounted for approximately 30 percent of the individuals represented in the Bell Cave avian samples. Although several species identified from the cave, e.g., *Accipiter striatus, Strix varia, Melanerpes carolinus, Cyanocitta cristata,* and *Pica pica,* often inhabit forest stands of mixed conifers and hardwoods, only the Ruffed Grouse appears generally restricted to brushy undergrowth associated with dense stands of coniferous forest.

Forests composed of jack pine (*Pinus banksiana* Lambert 1803), spruce (*Picea* Dietrich 1824), and fir (*Abies* Miller 1754) dominated the Midsouth during the full glacial (c. 22,000–16,500 B.P.) and were probably most similar to those of southern Manitoba today. This boreal-like climax forest was followed by late Wisconsinan mixed coniferous–deciduous forest that lasted from c. 16,500 to 12,550 B.P. (Delcourt, 1979). At Cheek Bend Cave, a deeply stratified upper Pleistocene–lower Holocene rockshelter deposit situated along the Duck River in Middle Tennessee, about 120 km NNE of Bell Cave, several species of rodents (Parmalee and Klippel, 1981a, 1981b), insectivores (Klippel and Parmalee, 1982), and birds (Parmalee and Klippel, 1982) reflected these boreal and related ecological conditions. Representative boreal species in the avifauna from Cheek Bend Cave included Boreal Owl (*Aegolius funereus* Linnaeus 1758), Northern Saw-whet Owl (*Aegolius acadicus* Gmelin 1788), Northern Hawk-Owl (*Surnia ulula* Linnaeus 1758), Gray Jay (*Perisoreus canadensis* Linnaeus 1766), and Pine Grosbeak (*Pinicola enucleator* Linnaeus 1758); remains of neither these nor other primarily boreal species were encountered in the Bell Cave avian assemblage. Nevertheless, several mammalian taxa represented at Bell Cave, including caribou, fisher, marten, least weasel (*Mustela rixosa* Bangs 1896), red squirrel (*Tamiasciurus hudsonicus* Erxleben 1777), and red-backed vole (*Clethrionomys gapperi* Vigors 1830) are indicative of boreal or more northern climatic conditions and vegetation communities that probably prevailed in northern Alabama for several millennia during the late Pleistocene.

At some period or periods during the time interval in which the cave was serving as a repository for faunal remains, or as a natural death trap for animals falling into fissures leading to the main room, extensive areas of grassland became established nearby. As mentioned earlier, remains of the thirteen-lined ground squirrel were recovered in strata in which those of *Tympanuchus* sp. cf. *T. cupido* occurred, suggesting well-established shortgrass prairie in the form of either open expanses or possibly savanna with scattered trees. An ecotone resulting from the junction of grassland and forest would have provided suitable habitat for many of the avian species represented in the Bell Cave assemblage. Waterfowl and various other species of aquatic and semi-aquatic birds would have occurred along the Tennessee River as migrants or winter residents; possibly some were permanent residents and nested in suitable local habitat. Three goose limb elements (cf. *Branta canadensis*) from the cave appeared to be those of a juvenile, based on the general porosity of the bones and the expanded articular ends that lacked complete ossification.

The question still remains as to the means by which such a variety of animals was entrapped or otherwise became a component of the Bell Cave bone assemblage. The possibility exists that a surface fissure (or fissures) may have been large enough to serve as a natural trap into which animals fell, or that predators living at or within these surface openings left the remains of their prey to fall or be washed eventually into the cave room. The size of the taxa represented in this cave fauna varied from that of warblers to black bear. In addition to birds and mammals, numerous remains of large individuals of aquatic turtles (*Chrysemys* Gray 1844; *Graptemys* Agassiz 1857; *Trionyx* Geoffroy St. Hilaire 1808) and fish (*Acipenser* Linnaeus 1758; *Ictalurus* Rafinesque 1820; *Moxostoma* Rafinesque 1820; *Aplodinotus* Rafinesque 1819) were also present in the deposit. The possibility exists that, in spite of their mobility, certain ground-dwelling birds such as grouse, quail, and turkeys might be more susceptible to natural entrapment. On the other hand, waterfowl and other aquatic birds, represented by at least 12 species at Bell Cave, as well as those species normally inhabiting the forest canopy, would not come within close proximity of fissure openings under natural conditions. The means by which animals ultimately became incorporated into the Bell Cave faunal assemblage probably varied during the more than 10,000 years of accumulation, but predation must have been a major factor.

The proximity of Bell Cave to the Tennessee River and the rugged limestone bluff in which it is located provided a diverse ecological setting for a varied avian fauna during the late Pleistocene. Imhof (1962:22) commented that "Wheeler National Wildlife Refuge [about 72 km east of Bell Cave] is probably the best inland area in Alabama for observing birds. Virtually the whole shoreline of the Tennessee River is excellent habitat with some places more attractive to woodland birds and others more attractive to water birds." One can only speculate as to general habitat conditions that prevailed during the period of bone accumulation at Bell Cave and the various local changes that undoubtedly took place from time to time. However, the presence in the principal bone-bearing strata of certain taxa, such as *Bonasa umbellus, Tympanuchus cupido, Ectopistes migratorius,* and representatives of the Anatidae, suggests diverse local habits, including riparian, forest, and grassland, that were favorable to resident populations as well as those of migrants at the end of the last glacial epoch.

With reference to the Bell Cave vertebrate faunal assemblage, as well as various others in eastern North America, the following statement by Wetmore (1959a:22) seems most appropriate: "The further contribution of paleornithology to the Pleistocene record will be in the discovery of additional extinct species and in further record of living forms. Details of chronology for the various levels of the Pleistocene will depend mainly on the mammals." Thus far, with the exception of certain boreal and grassland birds represented in the vertebrate assemblage from Cheek Bend Cave, Tennessee (Parmalee and Klippel, 1982), avian species represented in upper Pleistocene cave deposits in the Midwest and Southeast have exhibited little variation from the local modern bird assemblages. This may be attributable to the rarity of deeply stratified deposits containing major accumulations of bone, or perhaps the selective taphonomic processes that lead to the deposition and preservation of osteological remains. Although the statement by Wetmore (1959a) still appears valid, especially if one takes into account the small rodents and insectivores that are sensitive to and indicative of climatic and habitat changes, recovery of avian remains from the ever-growing number of excavated late Pleistocene sites in eastern North America should yield additional ecological and distributional data that will supplement, and perhaps complement, those suggested by mammalian assemblages.

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A LATE PLEISTOCENE AVIFAUNA FROM SAN MIGUEL ISLAND, CALIFORNIA

Daniel A. Guthrie

ABSTRACT. Upper Pleistocene deposits on San Miguel Island (12,000 B.P. and 25,000–39,000 B.P.) contain an avifauna comprising 41 species of birds, including 3 extinct species and 2 extinct subspecies. The paleoavifauna includes both pelagic and terrestrial species, the latter primarily raptoral birds, and it provides us with much new information on life on and around the northern Channel Islands of southern California in the late Pleistocene.

Key words: Pleistocene, avifauna, Channel Islands, evolution, biogeography.

INTRODUCTION

San Miguel Island, one of the northern Channel Islands located 50 km from the coast of southern California (Fig. 1) is well known for its archeological sites (Rozaire, 1976), and bird remains from these sites from 10,700 B.P. to Recent were described by Guthrie (1980). Pleistocene material from the island known prior to 1984 consisted of only a few isolated finds of mammoth, but reports by Johnson (1972) and by archeologists involved in survey work on the island indicated that bones were present in sediments below the earliest archeological sites. These reports led to a survey of San Miguel by the author during the summers of 1984 and 1985. The result was the discovery of several previously undescribed fossiliferous localities that contain abundant remains of birds. The geology of these deposits and their paleoavifauna is described here.

GEOLOGY

The basement rocks on San Miguel Island are Eocene and Miocene marine sediments and volcanics (Bremner, 1933). Prior to the late Pleistocene, a deep wave-cut bench was formed in these rocks, especially along the northwest-facing shores, the side most affected by prevailing winds. During the late Pleistocene, at times of slightly lowered sea level, this bench was covered by wind-blown sand from the nearby beaches on the northwest coast and by alluvium washed down from the island's interior.

Today, much of San Miguel is covered by a layer of wind-blown sand. However, on the northwest-facing slopes of the island, there are several pockets where wind erosion is uncovering upper Pleistocene deposits that are highly fossiliferous. Major collecting localities in these fossiliferous areas are shown in Fig. 1. More detailed information on fossil localities is on file at Channel Islands National Park headquarters in Ventura, California.

Radiocarbon (^{14}C) dates based on collagen from bones from several sites (Table 1) indicate two ages for the island's fossil material. Two fossil localities that are slightly inland and above the wave-cut bench (V-4, V-12) date about 12,000 B.P. All other localities are within the wave-cut bench and date between 25,000 and 39,000 B.P. These two periods of deposition correspond with times when sea level was at or near its current level (Curray, 1965; Vedder and Howell, 1980). A further indication that the upper Pleistocene deposits were formed near sea level is a layer of tar sand within the deposits at Cuyler Harbor (locality V-10). This layer was formed as a result of oil from a natural seep off the northwest shore of San Miguel Island washing up on the beach. This asphaltic layer, which dates to about 30,000 B.P., is

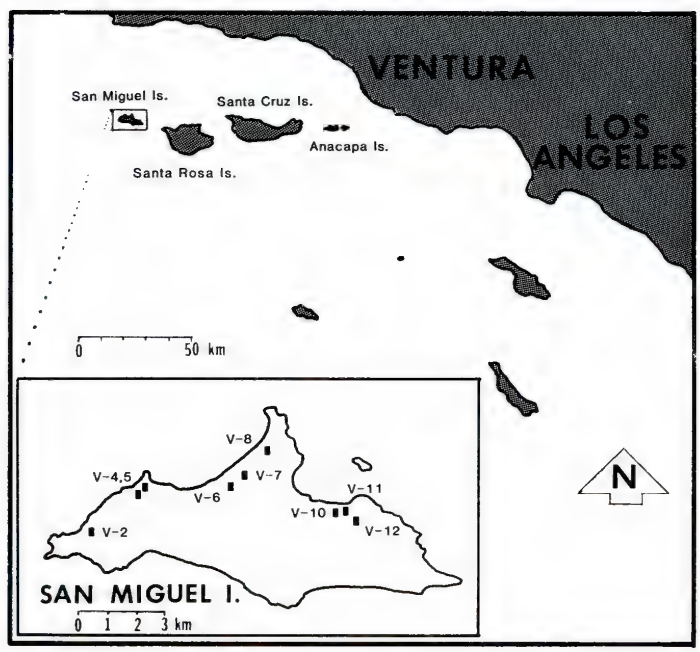

Figure 1. Map of the northern Channel Islands, with detail of San Miguel Island, showing fossil localities.

now about 15.5 m above current sea level. During the interval between the depositional dates (14,000–25,000 B.P.), sea level was much lower than today, and the shore of San Miguel Island, the source of depositional sand, would have been about 3 km away from the present northwest shore (Vedder and Howell, 1980). During this period, extensive soil layers that are generally unfossiliferous formed over much of San Miguel Island (Johnson, 1972, 1980).

Although the upper Pleistocene deposits on San Miguel Island are over 31 m thick and represent a considerable time period, the fauna within these deposits is rather uniform, and so far no changes in morphology or species composition have been detected. For this reason, the deposit is treated here as a single unit. Although over 95 percent of the vertebrate material from these deposits is avian, non-avian forms are also represented. The non-avian fauna, which is being described elsewhere (Guthrie, in press), consists of a rattlesnake, a lizard, two small rodents, a shrew, and dwarf forms of fox and mammoth. The only abundant invertebrate in the deposits is the terrestrial snail *Helminthoglypta ayresiana* (Newcomb 1861).

SYSTEMATICS

The classification system for Aves follows the 6th edition of the *Check-list of North American Birds* (American Ornithologists' Union, 1983). The collections are housed at the Santa Barbara Museum of Natural History (SBMNH) in Santa Barbara, California.

Class Aves

Order Gaviiformes

Family Gaviidae

Gavia arctica (Linnaeus 1758)

MATERIAL. Distal end of left tibiotarsus, SBMNH 26; right radius and 3 cervical vertebrae, SBMNH 44; thoracic vertebra, SBMNH 89.

REMARKS. *Gavia arctica* is known from Pleistocene deposits at San Pedro and Newport Bay, California (Howard, 1949: 22).

Order Podicepediformes

Family Podicipedidae

Podiceps nigricollis Brehm 1831

MATERIAL. Distal end of right humerus, SBMNH 23; proximal ends of left and right tarsometatarsi, SBMNH 13, 22.

REMARKS. These bones, although within the size range of *Podiceps nigricollis,* are small, a characteristic noted by Howard (1949:23) for bones referred to this species from the upper Pleistocene of San Pedro.

Aechmophorus sp. cf. *A. occidentalis* (Lawrence 1858) or *A. clarkii* (Lawrence 1858)

MATERIAL. Left carpometacarpus, SBMNH 20.

REMARKS. This bone measures 56.6 mm, about 5 percent larger than Recent material of these two species. Although the carpometacarpus is not identifiable to species, it is within the size range of the Pleistocene subspecies *Aechmophorus o. lucasi* L. Miller 1911 (Howard, 1949:22).

Table 1. Radiocarbon (^{14}C) dates from San Miguel Island. All dates corrected for $^{12}O/^{13}O$ ratios. Abbreviations: Beta, Beta Analytic, Coral Gables, Florida; AA, University of Arizona, Laboratory of Isotopic Geochemistry.

Identification No.	Locality	Level	Age (B.P.)	Material dated
Beta 14659	V-12	—	12,020 ± 270	*Chendytes lawi*
AA 1319	V-10	C	32,143 ± 787	*Chendytes lawi*
AA 1320	V-4	A	11,890 ± 95	*Fratercula* sp.
AA 1818	V-7	A	25,160	*Fratercula* sp.
AA 1819	V-7	C	>38,000	*Fratercula* sp.

Order Procellariiformes

Family Diomedeidae

Diomedea albatrus Pallas 1769

MATERIAL. Partial skull, SBMNH 56; left quadrate, SBMNH 21; distal end of left tibiotarsus, SBMNH 48; pelvic fragment, SBMNH 51; left carpometacarpus, SBMNH 61; right tarsometatarsus, SBMNH 65.

REMARKS. *Diomedea albatrus* was a common nearshore species prior to 1900, and it is well represented in Pleistocene marine deposits along the Pacific coast.

Family Procellariidae

Fulmarus glacialis (Linnaeus 1761)

MATERIAL. Two right humeri, SBMNH 33; distal end of a left humerus and 2 incomplete left ulnae, SBMNH 16; right humerus, SBMNH 161.

REMARKS. The humeri are 107.8 and 107.5 mm long, within the size range of Recent material of this species. The other bones are too fragmentary for measurement. This is another nearshore species common in Pacific coast marine Pleistocene deposits.

Puffinus griseus (Gmelin 1789)

MATERIAL. Right femur and distal end of left ulna, SBMNH 32; left tibiotarsus and tarsometatarsus, SBMNH 34; distal end of left humerus, right tarsometatarsus, and 2 left radii, SBMNH 40; right ulna, SBMNH 57; right humerus, coracoid, 2 right ulnae, and 2 right carpometacarpi, SBMNH 63.

REMARKS. This species is also known from upper Pleistocene deposits at Newport Bay (Howard, 1949:21).

Puffinus opisthomelas Coues 1864

MATERIAL. Right coracoid, SBMNH 3; left carpometacarpus, SBMNH 7; 2 left coracoids and 2 fragmentary left radii, SBMNH 78.

REMARKS. This species is known from several California Pleistocene deposits.

Family Hydrobatidae

Oceanodroma homochroa (Coues 1864)

MATERIAL. Left tarsometatarsus, SBMNH 163.

REMARKS. This species nests in small numbers on islands off the north shore of San Miguel Island (Sowls et al., 1980). It was previously unrecorded from Pleistocene deposits (Brodkorb, 1963:247).

Order Pelecaniformes

Family Pelecanidae

Pelecanus occidentalis Linnaeus 1766

MATERIAL. Thirteen cervical and thoracic vertebrae, SBMNH 56.

REMARKS. Bones of this species are unexpectedly rare in Pleistocene deposits (Brodkorb, 1963:267).

Family Phalacrocoracidae

Phalacrocorax penicillatus (Brandt 1837)

MATERIAL. Right carpometacarpus, SBMNH 18; distal end of left ulna, SBMNH 47; right coracoid, tibial shaft, and 2 cervical vertebrae, SBMNH 60.

REMARKS. Although *Phalacrocorax auritus* (Lesson 1831) is the commoner large cormorant in California coastal Pleistocene deposits (Howard, 1949:23), the San Miguel material is dominated by *P. penicillatus.*

Phalacrocorax pelagicus Pellas 1811

MATERIAL. Right quadrate, SBMNH 4; distal end of left coracoid, SBMNH 25; distal end of right tibiotarsus, SBMNH 162.

REMARKS. Although the specimens are fragmentary, all are at or just above the upper limit of size for Recent material of this species. The bones are of a different configuration and too small to be included in either *Phalacrocorax penicillatus* or *P. auritus.*

Order Ciconiiformes

Family Ardeidae

Ardea herodias Linnaeus 1758

MATERIAL. Fragmentary left humerus, right ulna, and right tibiotarsus, SBMNH 81.

REMARKS. The maximum width of the distal end of the humerus is 28.7 mm, which compares to measurements of 23.6–27.2 mm in Recent material. The proximal end of the ulna is missing, but this bone is shorter than Recent material, as indicated by the position of the attachments for the anterior articular ligament. Moreover, the anconal papillae are closer together than on Recent material. The position of the intermuscular line in Recent material crosses the ulna well proximal to the nutrient foramen, whereas on the specimen from San Miguel Island this line crosses distal to the nutrient foramen. The nutrient foramen is 155 mm from the distal end of the ulna on SBMNH 81, as compared with 122–146 mm in Recent material. Although the differences from Recent material noted here may merit at least subspecific rank, not enough material exists to warrant taxonomic designation.

This species, although previously unknown from marine Pleistocene deposits (Brodkorb, 1963:284), is not unexpected because it nests on San Miguel Island.

Family Plataliidae

Plegadis chihi (Vieillot 1817)

MATERIAL. Distal end of left humerus, SBMNH 100.

REMARKS. This species, unknown from marine deposits (Brodkorb, 1963:284), is present in the Pleistocene deposits at Rancho La Brea.

Order Anseriformes

Family Anatidae

Chen caerulescens (Linnaeus 1758)

MATERIAL. Proximal end of left humerus and phalanx 1 of digit 2, SBMNH 27; right mandible and carpometacarpus, SBMNH 41; proximal end of right humerus, SBMNH 54; right carpometacarpus and proximal end of left radius, SBMNH 66.

REMARKS. This species wintered regularly on the northern Channel Islands prior to 1900 (Guthrie, 1980).

Branta canadensis (Linnaeus 1758)

MATERIAL. Cranium, SBMNH 99; proximal end of left humerus, SBMNH 101.

REMARKS. The impressions of the salt glands above the orbit and overall size of the cranium are most like those in the small race of Canada Goose, *Branta canadensis minima* Ridgway 1885. Larger races of this species are common in the Pleistocene deposits of Santa Rosa Island (Orr, 1968).

Melanitta perspicillata (Linnaeus 1758)

MATERIAL. Distal end of left humerus, SBMNH 10.

REMARKS. This bone is slightly more robust than Recent material of this species, but it is not as large as in *Melanitta fusca.*

Melanitta fusca (Linnaeus 1758)

MATERIAL. Proximal end of right humerus, SBMNH 11; right coracoid, SBMNH 58.

REMARKS. This species is known from the Pleistocene of Newport Bay and San Pedro (Brodkorb, 1964:246).

Mergus serrator Linnaeus 1758

MATERIAL. Distal end of right ulna, SBMNH 12.

REMARKS. This species is previously unknown from the Pleistocene of California (Brodkorb, 1964:248), but it has been recovered from Pleistocene deposits at Fossil Lake, Oregon (Howard, 1946).

Table 2. Frequency of skeletal elements of *Chendytes lawi* from SMI-V-12.

Bone	Number	Percent
Femur	104	42.8
Tibiotarsus	30	12.3
Tarsometatarsus	13	5.3
Humerus	5	2.1
Ulna	2	0.8
Pelvis	9	3.7
Sternum	2	0.8
Coracoid	4	1.6
Scapula	1	0.4
Vertebra	71	28.8
Skull	3	1.2
Total	244	100.0

Chendytes lawi L. Miller 1925

MATERIAL. Humeri, 29; ulnae, 4; coracoids, 5; scapulae, 5; femora, 186; fibulae, 26; tibiotarsi, 101; tarsometatarsi, 40; phalanges, 22; pelvi and sacra, 29; sterna, 6; vertebrae, 423; skull fragments, 36; mandibulae, 8; quadrates, 12; pterygoids, 3; SBMNH 5, 35, 45, 49, 54, 59, 68, 70, 71, 73–75, 79, 82, 87, 94–96. Egg shell fragments, SBMNH 55, 69.

REMARKS. Bones of *Chendytes lawi* were found in small numbers at almost every locality. At two localities (V-10, V-12), *Chendytes* was very abundant and was the only species recovered at the latter site. Eggshell fragments of a thickness and curvature expected for a bird the size of *Chendytes* are abundant at both localities. This, and the recovery of numerous bones of immature individuals, indicates that these sites once hosted breeding colonies. Bones of *C. lawi* from locality V-12, radiocarbon (^{14}C) dated at 12,000 B.P., are the same size as material from northern California dated at 6000 B.P. (Morejohn, 1976) but slightly larger than the sample from San Miguel Island localities dating from 25,000 to 39,000 B.P. Measurements of specimens from various Pleistocene localities in California presented by Howard (1955) agree with those from the older San Miguel Island localities.

Although most skeletal elements are present, the frequency of different elements (Table 2) varies greatly. This variation is related to susceptibility to destruction by abrasion from wind-blown sand and to the collecting bias of surface collecting (Rich and Baird, 1986). Both of these biases favor preservation of thicker-walled and larger bones. In the case of *Chendytes*, these are leg bones. The preponderance of *Chendytes* leg bones found in midden sites was considered by Morejohn (1976) to indicate human-use patterns, but it is similar to that seen in deposits from San Miguel that were formed earlier than the oldest date for cultural material from the island.

Order Falconiformes

Family Vulturidae

Gymnogyps californianus amplus (L. Miller 1911)

MATERIAL. Right humerus and tibiotarsus, left radius and ulna, and partial cranium, SBMNH 97.

REMARKS. This material is similar to the specimens reported from Santa Rosa Island by Howard (Orr, 1968). Measurements are within the range of the Rancho La Brea species *Gymnogyps amplus*, or slightly larger (Table 3). However, recent work on condors by Emslie (1988) has indicated that there is much overlap between the Rancho La Brea sample of *G. amplus* and *G. californianus*. Emslie's assignment of all late Pleistocene material to the Recent species, with *amplus* retained as a subspecific designation, is followed here.

Table 3. Comparison of measurements (mm) of condor bones from San Miguel Island with Recent and Pleistocene samples.

	Origin of sample		
	Recent[a]	Rancho La Brea[a]	San Miguel Island
Humerus (maximum length)	262–274	260–292	300
Ulna (maximum length)	305–320	304–345	338
Tibiotarsus (maximum length)	208–213	212–244	245
Occipital (width)	22.5–24.9	25.6–30.2	28.4

[a] Data from Fisher, 1944, 1947.

Family Accipitridae

Haliaeetus leucocephalus (Linnaeus 1766)

MATERIAL. Distal end of left tibiotarsus, SBMNH 9; distal end of left tibiotarsus, SBMNH 24; right tarsometatarsus and distal end of right tibiotarsus, SBMNH 43; distal end of left tarsometatarsus, SBMNH 50; left tarsometatarsus and proximal left radius, SBMNH 62.

REMARKS. Prior to 1950 this species nested on San Miguel Island.

Buteo jamaicensis (Gmelin 1788)

MATERIAL. Claw and phalange, SBMNH 17; proximal left ulna, SBMNH 37; left humerus and distal right tibiotarsus, SBMNH 38; right humerus, SBMNH 46.

REMARKS. This species nests irregularly on San Miguel Island.

Family Falconidae

Polyborus plancus prelutosus Howard 1938

MATERIAL. Distal right tibiotarsus, SBMNH 36; pelvic fragments, SBMNH 80; proximal end of right tibiotarsus, SBMNH 84; distal end of left tibiotarsus, SBMNH 90; right tarsometatarsus, SBMNH 92; right radius, SBMNH 93; proximal end of right tarsometatarsus, SBMNH 98.

REMARKS. Maximum length of the measurable material from San Miguel is as follows: radius, 106.6 mm; tarsometatarsus, 93.5 mm; tibia, 110 mm. Howard (1938) described the Rancho La Brea caracara as a new species, *Polyborus prelutosus*, and more recently (Howard, 1962) assigned material from the upper Pleistocene of Santa Rosa Island to this species. She noted that *P. prelutosus* was "a link between the other known species" (Howard, 1938:238–39), i.e., *P. cheriway* (Jacquin 1784) of Central America and northern South America, *P. plancus* (J.F. Miller 1777) of southern South America, and *P. lutosus* Ridgway 1876 of Guadalupe Island. All three of these Recent forms are now

considered of subspecific rank within *P. plancus* (American Ornithologists' Union, 1983).

Howard (1938:239), in describing *Polyborus prelutosus*, noted that "were it not for the time element involved, all the caracaras might be thought of as purely subspecific divisions of one form." She went on to say, however, that "The idea of possible subspecific relationship between Pleistocene and Recent species seems to me to be wholly untenable" (Howard, 1938:239). Later, following the discussion of taxonomic approaches to chronoclinal variation by Simpson (1943), Howard (1947) and other avian paleontologists (e.g., Wetmore, 1959) recognized the applicability of subspecific names to fossil forms. Today the tendency is to identify fossil samples that differ slightly in size or robustness from Recent material of the same lineage simply as variant populations of the Recent species without a separate taxonomic designation (e.g., Howard, 1947). Even in cases where some bones are distinctly separable, if these bones are minor components, taxonomic designation is not made. However, in cases where such fossil samples were previously designated as separate species, the former species name is retained at the subspecific level, as was suggested by Wetmore (1959:12) and finally formally done by Emslie (1988) for *Gymnogyps californianus amplus*.

Given the range of variation in the Recent and Pleistocene samples of the genus *Polyborus* mentioned here and the lack of any single character where overlap between the samples does not occur, I consider designation of the Pleistocene population as a subspecies of the living caracara the best approach.

Falco sparverius Linnaeus 1758

MATERIAL. Proximal end of left humerus, SBMNH 19.

REMARKS. This species is a regular visitor to the northern Channel Islands.

Order Charadriiformes

Family Scolopacidae

Charadrius sp. cf. *C. alexandrinus* Linnaeus 1758 or *C. semipalmatus* Bonaparte 1825

MATERIAL. Right femur, SBMNH 83.

REMARKS. The femur is identical in size and configuration in these two small plovers. Although neither species is known from the North American fossil record, both species have been recovered from the South American Pleistocene (Campbell, 1976, 1979).

Family Laridae

Larus californicus Lawrence 1854

MATERIAL. Right tibiotarsus and tarsometatarsus, SBMNH 64; left humerus, SBMNH 67; right coracoid, SBMNH 28.

REMARKS. The coracoid and humerus are identical to Recent material of this species, whereas the tibiotarsus and tarsometatarsus are slightly shorter and more robust than Recent material. This species is also known from Pleistocene deposits at Fossil Lake, Oregon (Brodkorb, 1967:209).

Larus sp.

MATERIAL. Anterior sternal fragment, SBMNH 29.

REMARKS. This fragment could belong to any of four species of gulls (*Larus occidentalis* Audubon 1839, *L. argentatus* Pontoppidan 1763, *L. glaucescens* Naumann 1840, or *L. thayeri* Brooks 1915) present along the Pacific Coast.

Rissa tridactyla (Linnaeus 1758)

MATERIAL. Left coracoid, SBMNH 76.

REMARKS. The curvature of the sternal facet is identical to that of Recent material of this species and unlike that of other gulls of similar size (*Larus canus* Linnaeus 1758, *L. delawarensis* Ord 1815). This species is questionably recorded for Rancho la Brea (Howard, 1936:36).

Family Alcidae

Uria aalge (Pontoppidan 1763)

MATERIAL. Right ulna, SBMNH 2; left ulna and carpometacarpus, SBMNH 8; proximal end of right humerus, right ulna, and sacral fragment, SBMNH 14; left coracoid and femur, proximal end of left humerus, and premaxillary bones, SBMNH 42; right humerus, SBMNH 72.

REMARKS. Whereas the limb bones are identical to Recent material of this species, the premaxilla is slightly more robust. This species is also known from the Pleistocene of Santa Rosa Island (Orr, 1968).

Cepphus columba Pallas 1811

MATERIAL. Anterior portion of upper bill, SBMNH 15.

REMARKS. This specimen is slightly larger than Recent material of this species but the distance from the tip of the bill to the opening of the nares makes it clearly referrable here and not to *Uria aalge*, with which it otherwise might be confused because of size. *Cepphus columba* nests on San Miguel Island, but it is previously unrecorded in Pleistocene deposits (Brodkorb, 1967:219).

Synthliboramphus hypoleucus (Xantus de Vesey 1860)

MATERIAL. Bill tip, SBMNH 164; right humerus, SBMNH 165.

REMARKS. Both bones are slightly smaller than Recent material of *Synthilboramphus antiquus*, from which they are nearly indistinguishable in form. This species, which breeds today in small numbers on Prince Island just off the north shore of San Miguel Island (Sowls et al., 1980), has not been previously recorded in the Pleistocene of California (Brodkorb,1967:219).

Synthliboramphus antiquus (Gmelin 1789)

MATERIAL. Humeri, 102; ulnae, 58; radii, 12; carpometacarpi, 37; coracoids, 38; furculae, 10; scapulae, 2; femora, 5; tibiotarsi, 23; tarsometatarsi, 17; sacra; pelvi, 2; sterni, 4; vertebrae, 6; skull fragment; quadrate; SBMNH 166–176.

REMARKS. The bones referred to *Synthliboramphus antiquus* are slightly larger than Recent material of this species. Bones of this species are separable on the basis of size from *S.*

Table 4. Measurements of depth of maxilla in puffins. All measurements taken at anterior edge of external nares. All samples represent both sexes.

Species	N	Range	Mean	SD
Cerorhinca monocerata	12	5.91–7.70	7.09	0.46
Fratercula sp.	12	8.86–10.34	9.52	0.40
Fratercula cirrhata	11	12.40–16.60	14.61	1.18

hypoleucus, which they otherwise resemble in all respects. The presence of bones from immature individuals, as indicated by degree of ossification, and of eggshell fragments assignable to this species on the basis of curvature and thickness suggest that a breeding population is sampled by this collection. This species is an uncommon wintering species south of central California today, but it is present in upper Pleistocene deposits at San Pedro (Brodkorb, 1967:219).

Ptychoramphus aleuticus (Pallas 1811)

MATERIAL. Humeri, 289; ulnae, 203; radii, 58; carpometacarpi, 118; coracoids, 135; furculae, 9; scapulae, 7; femora, 59; tibiotarsi, 82; tarsometatarsi, 48; sacra, 3; pelvi, 2; sterni, 14; vertebrae, 18; skull fragments, 10; mandible; quadrates, 4; SBMNH 177–190.

REMARKS. As an estimated 20,000 *Ptychoramphus aleuticus* nest on Prince Island and another 2,000 on Castle Rock, both just off the north shore of San Miguel Island (Sowls et al., 1980), the presence of this species in San Miguel Island deposits is not unexpected. As with the previous species, the presence of bones from immature birds and of eggshell fragments referrable to this species indicate that it nested on San Miguel Island. The bones referred here are slightly larger than Recent material of this species from southern California.

Fratercula sp.

MATERIAL. Humeri, 501; ulnae, 381; radii, 97; carpometacarpi, 256; coracoids, 373; furculae, 41; scapulae, 43; femora, 181; tibiotarsi, 107; tarsometatarsi, 124; phalanges, 103; claws, 21; sacra, 27; pelvi, 11; sterni, 52; vertebrae, 227; skull fragments, 67; mandibuli, 28; quadrates, 29; SBMNH 141–144, 147–160.

REMARKS. This species, which is being described elsewhere, is the most abundant species in the upper Pleistocene deposits on San Miguel Island, the bones of this puffin literally forming a pavement at locality 7. The presence of eggshell fragments, remains of immature individuals, and complete articulated skeletons, which apparently are the remains of animals that died in burrows, all indicate that these remains are from a breeding colony. At first, the postcranial bones were thought to belong to the living species *Cerorhinca monocerata* (Pallas 1811), from which they are almost indistinguishable on the basis of size and form. It was not until a skull was recovered that a significant difference from *C. monocerata* in the height of the mandibles and maxillaries became apparent. Because all maxillae recovered from the upper Pleistocene deposits on San Miguel Island are referrable to *Fratercula* sp. on the basis of size (Table 4), all postcranial material is also referred to that genus here, despite the fact that many elements are inseparable from *C. monocerata*.

The great similarity of the postcranial elements of *Cerorhinca monocerata* to those of *Fratercula* sp. and the age of the deposits on nearby Santa Rosa Island make it likely that postcranial elements from Santa Rosa Island referred to *C. monocerata* by Howard (in Orr, 1968) belong to *Fratercula* sp. With this reassignment, *Cerorhinca monocerata* is completely absent from the fossil record and is known back to only 2,000 B.P. in midden deposits on San Miguel Island (Guthrie, 1980).

The great skeletal similarities between *Fratercula* sp. and *Cerorhinca monocerata* lead me to consider it highly likely that the former was ancestral to the latter. This view, if correct, calls into question the assignment of Miocene and Pliocene material to *Cerorhinca* (L. Miller, 1925; Howard, 1971).

Order Strigiformes

Family Tytonidae

Tyto alba (Scopoli 1769)

MATERIAL. Proximal end of right femur, SBMNH 6; shaft of left humerus, SBMNH 30.

REMARKS. These bones are identical to Recent material of this species.

Family Strigidae

Asio sp. cf. *A. priscus* Howard 1964

MATERIAL. Distal end of left femur, SBMNH 86.

REMARKS. Howard (1964) described *Asio priscus* based on a tibiotarsus from the upper Pleistocene of Santa Rosa Island. Her diagnosis indicated that *A. priscus* was generally distinguishable from *A. flammeus* Pontoppidan 1763 by size, the fossil bone being 6 mm (7 percent) longer than that of Recent *A. flammeus* and also longer than specimens assigned to *A. flammeus* from upper Pleistocene deposits of Rancho La Brea. The femur from San Miguel Island is slightly larger than material of Recent *A. flammeus* available to me, and it also has a straighter shaft. Although *A. flammeus* is a regular visitor to the Channel Islands during migration (Garrett and Dunn, 1980) and is also known from midden deposits on San Miguel Island (Guthrie, 1980), this specimen seems best assigned to the slightly larger island species *A. priscus*.

Order Passeriformes

Family Alaudidae

Eremophila alpestris (Linnaeus 1759)

MATERIAL. Right tarsometatarsus, SBMNH 88.

REMARKS. This species nests on San Miguel Island.

Family Corvidae

Corvus corax Linnaeus 1758

MATERIAL. Left femur and right radius, SBMNH 39; proximal left humerus, right and left tarsometatarsi, and fragment of left carpometacarpus, SBMNH 31.

REMARKS. This species nests on San Miguel Island.

Table 5. Avifauna from upper Pleistocene deposits on San Miguel Island. Numbers indicate identifiable bones from each locality.

Species	Locality number								
	2	4	5	6	7	8	10	11	12
Gavia arctica	—	1	—	—	3	—	1	—	—
Podiceps nigricollis	—	—	1	—	1	—	1	—	—
Aechmophorus sp.	—	—	—	—	1	—	—	—	—
Diomedea albatrus	—	1	1	3	1	—	—	—	—
Fulmarus glacilais	—	1	—	—	3	—	—	—	—
Puffinus griseus	—	6	1	—	8	—	—	—	—
Puffinus opisthomelas	—	2	—	—	1	—	1	—	—
Oceanodroma homochroa	—	—	—	—	1	—	—	—	—
Pelecanus occidentalis	—	12	—	—	—	—	—	—	—
Phalacrocorax penicillatus	—	4	—	1	1	—	—	—	—
Phalacrocorax pelagicus	—	—	—	2	1	—	—	—	—
Ardea herodias	—	4	—	—	—	—	—	—	—
Plegadis chihi	—	—	—	—	1	—	—	—	—
Chen caerulescens	—	—	—	—	4	1	1	—	—
Branta canadensis	—	—	—	1	1	—	—	—	—
Melanitta perspicillata	—	—	—	—	—	—	1	—	—
Melanitta fusca	—	—	—	—	1	—	1	—	—
Mergus serrator	—	—	—	—	—	—	1	—	—
Chendytes lawi	1	1	1	3	4	—	667	16	244
Gymnogyps californianus	—	—	—	—	—	—	6	—	—
Haliaeetus leucocephalus	—	—	—	—	7	—	2	—	—
Buteo jamaicensis	—	1	—	—	4	—	1	—	—
Polyborus plancus	—	1	—	2	4	—	—	—	—
Falco sparverius	—	—	—	—	1	—	—	—	—
Charadrius sp.	—	—	—	—	—	—	1	—	—
Larus californicus	—	—	—	—	2	—	—	2	—
Larus sp.	—	1	—	—	—	—	—	—	—
Rissa tridactyla	—	1	—	—	—	—	—	—	—
Uria aalge	—	—	—	4	4	1	—	1	—
Cepphus columba	—	—	—	—	1	—	—	—	—
Synthliboramphus hypoleucus	—	—	—	—	1	—	1	—	—
Synthliboramphus antiquus	—	15	—	34	161	15	87	7	—
Ptychoramphus aleuticus	—	69	10	124	107	5	612	24	—
Fratercula sp.	93	232	61	—	1,166	61	1,032	24	—
Tyto alba	—	—	—	—	1	—	—	—	—
Asio sp. cf. *A. priscus*	—	—	—	—	—	—	1	—	—
Eremophila alpestris	—	—	—	—	—	—	1	—	—
Corvus corax	—	—	—	—	2	—	4	—	—
Zonotrichia leucophrys	—	—	—	—	1	—	—	—	—
Melospiza melodia	—	—	—	—	1	—	—	—	—
Passeriformes	—	—	—	—	2	—	—	—	—

Family Emberizidae

Zonotrichia leucophrys (Forster 1772)

MATERIAL. Left tibiotarsus, tarsometatarsus, and proximal end of left ulna, SBMNH 145.

REMARKS. This species is a common winter visitor to San Miguel Island.

Melospiza melodia (Wilson 1810)

MATERIAL. Right ulna, left tibiotarsus, left mandible, and proximal end of left humerus, SBMNH 146.

REMARKS. This species nests on San Miguel Island.

Passeriformes indet.

MATERIAL. Distal tibia and pelvic fragment, SBMNH 77.

DISCUSSION

The upper Pleistocene terrestrial fossil-bearing deposits on San Miguel Island were formed by erosion from cliffs just inland from the shoreline and wind deposition of sand blowing inland from beaches. Thus, the deposits contain representatives of the avifauna that both nested on these cliffs and washed up on the beaches and were blown inland (Table 5). The terrestrial paleoavifauna consists of 11 species, seven raptors and four passeriforms. All but three of these species are present regularly on San Miguel Island today. Of the three species not present today,

two (*Haliaeetus leucocephalus, Gymnogyps californianus*) are known either historically or from archeological sites on San Miguel Island and one (*Polyborus plancus*) is known from fossil sites on nearby Santa Rosa Island. With the exception of *Gymnogyps californianus* and *Polyborus plancus,* all of the raptoral species in the paleoavifauna either nest on San Miguel Island or did so in historic time. *Polyborus plancus* has colonized islands elsewhere off the Pacific coast. The small number of bones recovered of these raptoral species is consistent with their small island populations. Bones of land birds are rare in the deposits. They tend to be associated with bones of mice and *Tyto alba,* and they probably represent the remains of owl pellets.

The marine paleoavifauna, with three exceptions, consists of species that either occurred in historic time or currently occur in the vicinity of San Miguel Island. As indicated here, all three of the exceptions apparently nested on San Miguel Island. One, *Chendytes lawi,* is extinct with no descendents. The other two species (*Synthliboramphus antiquus* and *Fratercula* sp.) or their descendents today breed well north of San Miguel Island.

The abundance of three species of alcids (*Fratercula* sp., *Synthliboramphus antiquus,* and *Ptychoramphus aleuticus*) and the duck *Chendytes lawi* as well as eggshells and bones of immature individuals referrable to these species indicates presence of nesting colonies on San Miguel Island. Variation in the numbers of these four species among the various fossil localities is probably a reflection of the nearness of the colonies to the different localities and an indication that each species nested in a slightly different area These colonies may have suffered predation by the Pacific rattlesnake [*Crotalus viridis* (Rafinesque 1818)] and island fox [*Urocyon littoralis* (Baird 1858)], both of which were present on San Miguel as well as from raptoral birds. The dwarf mammoth [*Mammuthus exilis* (Stock and Furlong 1928)] may also have affected nesting success by walking on nests and collapsing burrows. These factors may have been partially responsible for the large numbers of these species in the deposits.

Marine species that did not nest on San Miguel Island in large colonies are rare in the deposit. Bones of most of these species are incorporated in the deposit either because they served as food for raptoral birds nesting on San Miguel Island or because their bones blew inland from beached carcasses. *Phalacrocorax pelagicus* and *Cepphus columba* nest on San Miguel Island in sea caves overhanging the sea. Both species are rare in San Miguel Island deposits, as would be expected because incorporation of bones from these species into the deposits would have been primarily from beached birds rather than directly from nesting colonies.

Two of the species in the San Miguel Island paleoavifauna (*Oceanodroma homochroa, Cepphus columba*) are recorded for the first time in the late Pleistocene. Four additional species (*Mergus serrator, Larus californicus, Charadrius* sp., and *Synthliboramphus hypoleucus*) are new to the California Pleistocene.

Only two species in the San Miguel Island paleoavifauna represent extinct lineages. One, *Chendytes lawi,* was a flightless duck that became extinct only after human occupation of the northern Channel Islands (Guthrie, 1980). The other, *Asio priscus,* is an extinct island endemic closely related to the mainland *Asio flammeus.* In the approximately 30,000 years since the formation of the San Miguel Islands upper Pleistocene deposits, one species (*Fratercula* sp.) has changed at the generic level and an additional two species (*Gymnogyps californicus amplus, Polyborus plancus prelutosus*) have changed at the subspecific level. Both these latter subspecies were once considered separate species.

The number of extinct species from the upper Pleistocene of San Miguel Island (2 of 41 or 5 percent) is low compared to the Pleistocene terrestrial deposits, which contain large numbers of extinct raptors (Selander, 1965), but it agrees with the number of extinct forms (3 of 41 species) from other upper Pleistocene marine deposits in California (Howard, 1949).

Although only three of the species of late Pleistocene birds from San Miguel Island that belong to extant lineages are taxonomically separated from Recent populations, 13 of 41 species in the paleoavifauna are separable on the basis of size or configuration. Of these, 12 are larger than their modern representatives and 1 is smaller. Zink and Remsen (1986) recently reviewed the application of Bergman's rule to birds and found few species that supported the rule and two alcids that contradicted it. However, R. Storer (pers. comm., 1988) has found north–south clinal variation in birds to be more prevalent than previously thought. He also finds significant clinal variation in two alcids, a guillemot and a murre. The larger size of many of the late Pleistocene birds on San Miguel Island may be correlated with cooler climates at the time of deposition. The one species that is smaller in the late Pleistocene than its Recent descendents (*Synthliboramphus hypoleucus*) had a larger member of the same genus also present on the island. Smaller size here may be the result of interspecific competition. That five of the six species of alcids from the upper Pleistocene of San Miguel Island are separable from Recent forms suggests a high rate of evolution in the group.

SUMMARY

Previously known Pleistocene deposits from offshore California are either marine with few birds, or, as is the case with the extensive deposits on Santa Rosa Island, they contain a mainly terrestrial and lagoonal avifauna (Orr, 1968). The upper Pleistocene deposits along the northwestern coast of San Miguel Island contain a well-preserved and incredibly abundant avifaunal assemblage with 41 species and provide us with our most complete record of a coastal avifauna in southern California during the late Pleistocene.

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NEW SPECIES OF *GALLICOLUMBA* AND *MACROPYGIA* (AVES: COLUMBIDAE) FROM ARCHEOLOGICAL SITES IN POLYNESIA

David W. Steadman

ABSTRACT. *Gallicolumba nui* new species is described from 280 bones (14 different elements) recovered from archeological sites up to 2,000 years old on the islands of Ua Huka, Hiva Oa, and Tahuata (Marquesas Islands), Huahine (Society Islands), and Mangaia (Cook Islands). This largest of all "ground-doves" probably occurred on many East Polynesian islands before human activities caused its demise. Throughout East and West Polynesia today, *Gallicolumba* is absent from most islands and, where it occurs, only a single species is present. At least two species of *Gallicolumba* coexisted on Ua Huka, Hiva Oa, Tahuata, Huahine, and Mangaia; presumably the same was true on many other East Polynesian islands. *Macropygia heana* new species is described from 199 bones (15 different elements) recovered from the Hane Archeological Site, Ua Huka, Marquesas Islands. *Macropygia arevarevauupa* new species is described from a single distinctive tibiotarsus from the Fa'ahia Archeological Site, Huahine, Society Islands. Compared to all other "cuckoo-doves," both *M. heana* and *M. arevarevauupa* had long, slender legs. They are also the only species of *Macropygia*, living or extinct, known from Polynesia. Vanuatu is the nearest locality inhabited by any species of *Macropygia* today. Other extinct populations or species of *Macropygia* undoubtedly await discovery on the hundreds of islands between Vanuatu and Ua Huka or Huahine.

The diversity of pigeons and doves in Polynesia has been reduced greatly by human activities. On Ua Huka and Huahine, where only one species of columbid survived into the time of European contact (*Ptilinopus dupetithouarsii* and *P. purpuratus*, respectively), six species in four genera (*Gallicolumba, Macropygia, Ptilinopus, Ducula*) existed when the first Polynesians arrived 2,000 years ago. On Mangaia, where no columbids are known historically, five species in three genera (*Gallicolumba, Ptilinopus, Ducula*) were present when Polynesians first arrived.

Key words: Polynesia, archeology, Columbidae, doves, island extinctions.

INTRODUCTION

The genus *Gallicolumba* Heck 1849, usually referred to as "ground-doves," consists of about 19 species that collectively are found from the Philippines and Sulawesi eastward through Oceania to the Marquesas Islands and Tuamotu Archipelago (Peters, 1937:133–37; Goodwin, 1967:264–84; Fig. 1 herein). Very little is known about the ecology and behavior of these ground-dwelling pigeons of tropical forests. The most detailed ecological and behavioral information on *Gallicolumba* and the best photographs are those of Coates (1985:282–88) for *G. rufigula* Pucheran 1853, *G. beccarii* (Salvadori 1875), and *G. jobiensis* (Meyer 1875) of New Guinea. Within Polynesia, *Gallicolumba* is represented by three species of limited distribution (duPont, 1976; Holyoak and Thibault, 1984; Pratt et al., 1987): *G. rubescens* (Vieillot 1818) from three islands in the Marquesas; *G. erythroptera* (Gmelin 1789) from Tahiti and Mo'orea in the Society Islands and numerous islands in the Tuamotu Archipelago; and *G. stairii* (G.R. Gray 1856) from islands scattered through Fiji, Tonga, Samoa, Wallis, and Futuna. Considering the well-documented vulnerability of insular birds to human-caused extinction, the limited and discontinuous ranges of these three species suggest that they each once occupied more islands than at present. Bones from archeological sites spanning the past 2,000 years now show this to be the case. Furthermore, such bones reveal the former existence of an undescribed species of *Gallicolumba* that was larger than all congeners and was sympatric with *G. rubescens* and *G. erythroptera*.

The genus *Macropygia* Swainson 1837, usually referred to as "cuckoo-doves" because of their long tails and relatively slender overall appearance, consists of about eight arboreal species that are found in tropical forests from Southeast Asia and the Philippines through Indonesia, New Guinea, and eastern Australia eastward to the Solomon Islands and Vanuatu (Peters, 1937:75–81; Goodwin, 1967:147–59; Fig. 1 herein). Thus there are no species of *Macropygia* in Polynesia today. As with the ground-doves, the ecology and behavior of cuckoo-doves are little known, the most detailed information being that of Coates (1985:263–66) for *M. amboinensis* (Linnaeus 1766), *M. nigrirostris* Salvadori 1875, and *M. mackinlayi* Ramsay 1878 of New Guinea, and that of Frith (1982:143–50) for *M. phasianella* (Temminck 1821) of eastern Australia (also see Goodwin, 1967: 147–59). Based on similarities in plumage and tail shape, the genus *Reinwardtoena* Bonaparte 1854 (three species from New Guinea, Bismarck Archipelago, and Solomon Islands) seems to be closely related to *Macropygia* (Goodwin, 1967:148). The osteology of *Reinwardtoena*, described later, corroborates this suggestion.

METHODS AND MATERIALS

Comparative skeletons used in this study are from the bird collections of the American Museum of Natural History (AMNH), Delaware Museum of Natural History (DMNH), United States National Museum of Natural History (USNM),

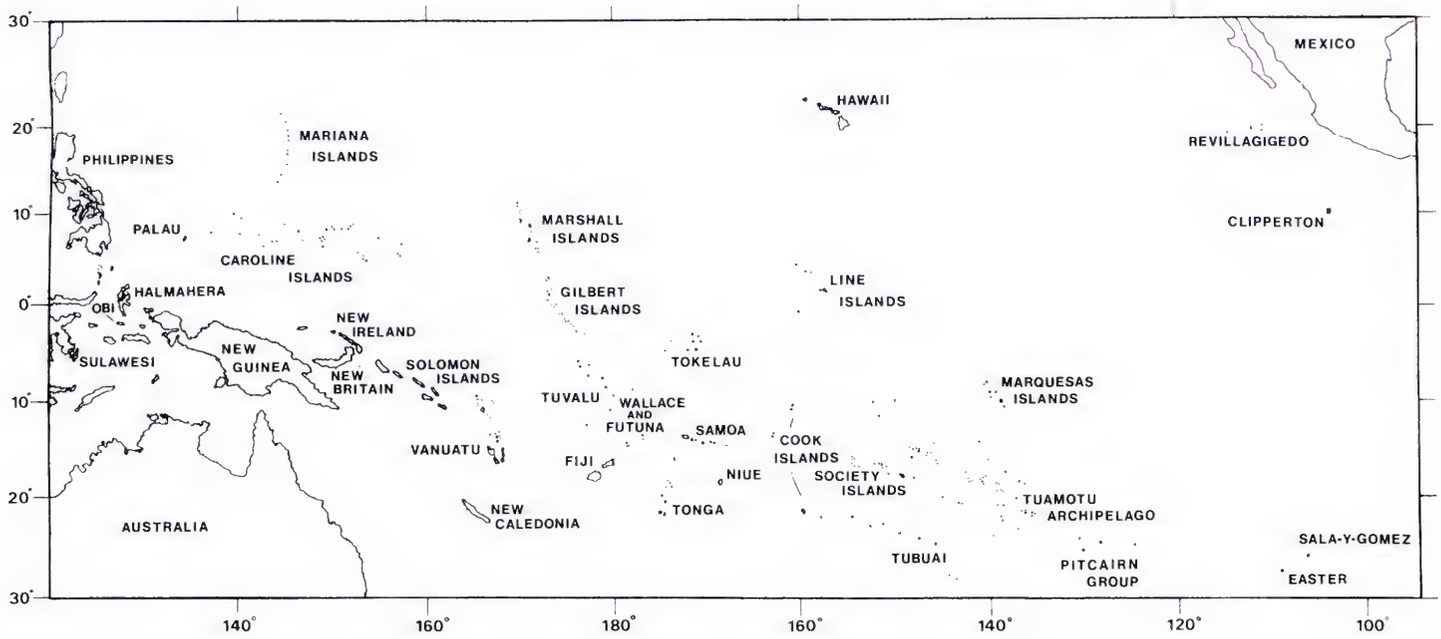

Figure 1. The tropical Pacific Ocean, with names of all island groups mentioned in the text, figures, and tables. See Figs. 6–9 for detail maps of East Polynesian island groups.

and University of Washington Thomas Burke Memorial Washington State Museum (UWBM). Archeological bones are from the Department of Vertebrate Zoology, Bernice P. Bishop Museum, Honolulu (BPBM), département d'Archéologie de Polynésie, Tahiti (DAPT), Institut de Paléontologie, Muséum national d'Histoire naturelle, Paris (NCP), USNM Division of Vertebrate Paleontology, and UWBM Fossil Bird Collection. Osteological nomenclature generally follows that of Baumel et al. (1979). Measurements were taken with digital calipers with 0.01 mm increments, rounded to the nearest 0.1 mm.

Most of the osteology and systematics in this paper are based upon study of the tarsometatarsus and tibiotarsus, for three reasons: (1) these two bones typically occur abundantly in archeological sites; (2) within Pacific columbids, these two elements have many diagnostic characters; and (3) for many modern species, the only comparative bones available are those that can be removed from the legs of study skins, namely the tarsometatarsus and tibiotarsus.

SYSTEMATICS

Class Aves Linnaeus 1758

Order Columbiformes Latham 1790

Family Columbidae Illiger 1811

Genus *Gallicolumba* Heck 1849

The holotype and paratype tarsometatarsi are referred to the genus *Gallicolumba* rather than to the other genera of columbids in Oceania (*Columba* Linnaeus 1758, *Ducula* Hodgson 1836, *Ptilinopus* Swainson 1825, *Didunculus* Peale 1848, *Chalcophaps* Gould 1843, *Macropygia*, and *Caloenas* G.R. Gray 1840) because of the following unique combination of characters: overall shape narrow and elongate; intercotylar tuberculum large; foramina vascularia proximalia small; proximomedial portion of the shaft shallow in medial aspect; proximodorsal surface of shaft not highly excavated; plane of trochleae highly curved in distal aspect.

Gallicolumba nui new species

Figures 2, 3; Tables 1–3

HOLOTYPE. BPBM 176000, tarsometatarsus lacking crista hypotarsi.

DIAGNOSIS. Tarsometatarsus larger than any other species of *Gallicolumba* (Table 2; Fig. 2). Medial foramen vasculare proximale and foramen vasculare distale larger than in all other species. Medial margin of proximal one-third of corpus tarsometatarsus convex rather than concave. Differs further from *Gallicolumba longitarsus* Balouet and Olson 1989 of New Caledonia as follows: intercotylar tuberculum larger; crista hypotarsi longer; corpus tarsometatarsus stouter and less straight; proximomedial one-third of corpus tarsometatarsus more shallow in medial aspect; distolateral two-thirds of corpus tarsometatarsus deeper in lateral aspect; lateral foramen vasculare proximale smaller; fossa metatarsi I longer; middle trochlea broader and shorter; lateral trochlea broader.

TYPE LOCALITY AND HORIZON. Hane Site, MUH-1 (also known as "Hane Dune Site"), Ua Huka, Marquesas Islands (Fig. 6), Layer V, Area B, collected in 1964–1965 by Yosihiko H. Sinoto and associates.

TOPOTYPICAL PARATYPES. 47 tarsometatarsi, BPBM 162536–162538, 162607–162609, 162938, 163013–163016, 163133, 163134, 163250, 163314, 163326, 163327, 163469, 168973, 168981, 168984, 169069, 169070, 169089–169091, 169093, 169478, 169806–169809, 171171, 171378, 171884, 172203, 173492–173494, 173496, 173681, 174431, 174885, 175334, 176266, 180336, 181063.

REFERRED MATERIAL. Hane Site (MUH-1), Ua Huka, Marquesas Islands (Fig. 6): mandible (BPBM 169000); 2 sterna

Table 1. **Bones of *Gallicolumba nui*, by element and island. All specimens are from archeological sites. Numbers refer to the number of identified specimens. Abbreviations: CI, Cook Islands; MI, Marquesas Islands; SI, Society Islands.**

	Ua Huka MI	Hiva Oa MI	Tahuata MI	Huahine SI	Mangaia CI	Total
Mandible	1					1
Sternum	2					2
Furcula			1			1
Coracoid	35	6		2	2	45
Scapula	28	5			1	34
Humerus	22	6				28
Ulna	20	2			2	24
Radius	11	1				12
Ulnare	1					1
Carpometacarpus	6					6
Phalanx digitalis majoris I	2	1		1		4
Femur	15	3			1	19
Tibiotarsus	40	9				49
Tarsometatarsus	48	5				53
Total	232	38	1	3	6	280

(BPBM 176297, 181295); 36 coracoids (BPBM 162522–162525, 162594, 162744, 163006, 163007, 163131, 163298, 163321, 165512, 165533, 165534, 165566, 168995, 169001, 169122, 169794, 169811, 170673, 171880, 171894, 173568–173570, 174072, 174423, 174504, 174509, 175329, 176007, 176291, 176292, 180322, 181065) [six of the coracoids (BPBM 162744, 163298, 165512, 165533, 165534, 165566) were incorrectly reported as belonging to a new species of parrot, *Vini sinotoi*, by Steadman and Zarriello (1987)]; 28 scapulae (BPBM 162526, 162611, 162945, 163008, 163237, 163307, 163322, 168988, 168992–168994, 169124, 169481, 169482, 171882, 171890, 173550–173552, 173775, 175055, 175225, 175324, 176063, 176296, 176299, 180335, 180489); 22 humeri (BPBM 162527, 163010, 169483, 169486, 169798, 173626, 173939, 174875, 175054, 175335, 176055, 176262, 176263, 176265, 176689, 180328–180331, 180340, 181296, 181305); 20 ulnae (BPBM 162528, 163316, 168975, 168979, 169086, 169472, 173615–173619, 173940, 173944, 174096, 174786, 175394, 176268, 180325, 181064, 181275); 11 radii (BPBM 162529, 162596, 163325, 168976, 172207, 173649, 173662, 173672, 173807, 173946, 180334; ulnare (BPBM 163700); 6 carpometacarpi (BPBM 163011, 165498, 169484, 171879, 171887, 173639); 2 phalanx digitalis majoris I (BPBM 174420, 175323); 15 femora (BPBM 162597, 162616, 163114, 168974, 168980, 168982, 168998, 169068, 169087, 169092, 169810, 170682, 174426, 174435, 175373); 40 tibiotarsi (BPBM 162530–162535, 162600–162605, 162952, 163038, 163132, 168983, 169067, 169474, 169799–169801, 169803, 169804, 170670, 173175, 173539, 173900, 174444, 174445, 175234, 176272, 176274, 176629, 176630, 176982, 180337–180339, 181066, 181485).

Hanatekua Shelter No. 2 Site (MH-11, =MH-3-12), Hiva Oa, Marquesas Islands (Fig. 6): 5 tarsometatarsi (BPBM 165668, 167246, 167280, 167303, 167352); 6 coracoids (BPBM 165645, 167240, 167251, 167264, 167265, 167297) [BPBM 165645 was incorrectly reported as belonging to a new species of parrot, *Vini sinotoi*, by Steadman and Zarriello (1987)]; 5 scapulae (BPBM 167278, 167308, 167334, 167337, 167355); 6 humeri (BPBM 167245, 167339–167343); 2 ulnae (BPBM 165659, 167273); radius (BPBM 167289); phalanx digitalis majoris I (BPBM 168277); 3 femora (BPBM 167244, 167298, 168277); 9 tibiotarsi (BPBM 165661, 167237, 167239, 167242, 167243, 167257, 167281, 167347, 167348).

Hanamiai Site (MT-1), Square M11, Layer H28, depth 242–245 cm, Tahuata, Marquesas Islands (Fig. 6): furcula (BPBM 166789).

Fa'ahia Site (ScH 1-2), Huahine, Society Islands (Fig. 7): 2 coracoids (BPBM 168126, DAPT 120); phalanx digitalis majoris I (DAPT 22).

Te Rua Rere Cave, Mangaia, Cook Islands (Fig. 8): 2 coracoids (USNM 402841, 402842); scapula (USNM 402839).

Tangatatau Rockshelter (MAN-44), Mangaia, Cook Islands: 2 ulnae (UWBM 1314, 1384).

Tuatini Cave, Mangaia, Cook Islands: femur (USNM 402838).

ETYMOLOGY. From the widespread Polynesian word *nui*, which means "great, large" (London Missionary Society, 1851: 156), "immense, very great, very large" (Savage, 1980:185). As used here, *nui* refers to the vast geographical range of *Gallicolumba nui* as well as to the large size of the bird itself.

DESCRIPTION. The elements of *Gallicolumba nui* other than the tarsometatarsus, listed earlier, are referred to *Gallicolumba* rather than to *Columba, Ducula, Ptilinopus, Macropygia, Chalcophaps, Didunculus*, or *Caloenas* because of the following characters. Within *Gallicolumba*, all of these specimens are referred to *G. nui* on the basis of their large size.

Mandible. Ventral margin of os prearticulare sharper.

Sternum. Spina interna narrower, with four symmetrical projections; crista lateralis narrower, forming a more acute angle with plane of the dorsal surface.

Coracoid. Processus acrocoracoideus more elongate, narrow, and pointed in dorsal aspect; depression between corpus coracoideus and dorsal margin of facies articularis humeralis deeper; corpus coracoideus broader and more gradually tapered; impressio musculo sternocoracoideus shallower.

Scapula. Cranial margin of facies articularis humeralis rounder (less notched); ventral margin of facies articularis humeralis more pointed; medial surface of tuberculum coracoideum smaller and less concave.

Humerus. Caput humeri more pointed and with distinct knob on caudal surface of distal portion; sulcus ligamentum transversus deeper.

Table 2. Measurements (mm) of the tarsometatarsus of *Gallicolumba* spp., with mean, range, and sample size. Abbreviations: F, female; M, male; U, sex unknown. Specimen numbers are given for archeological specimens only.

	Total length	Proximal width	Least width of shaft	Least depth of shaft	Distal width
Gallicolumba nui Holotype, Hane Site, Ua Huka, Marquesas (U) BPBM 176000	51.5 1	9.0+ 1	3.9 1	2.7 1	9.6 1
Gallicolumba nui Paratypes, Hane Site, Ua Huka, Marquesas (28U) BPBM 162537, 162538, 162607–162609, 163013–163016, 163133, 163326, 163327, 163469, 168973, 168981, 168984, 169069, 169070, 169478, 169808, 171378, 171884, 173492, 173494, 174431, 176266, 180336, 181063	— 	9.9 1	3.7 3.4–4.2 17	2.6 2.5–2.9 26	9.4 9.1–10.2 5
Gallicolumba nui Hanatekua Shelter No. 2, Hiva Oa, Marquesas (4U) BPBM 165668, 167246, 167303, 167352	50.4+ (est. 53) 1	9.2 9.2–9.3 2	3.7 3.5–3.9 3	2.8 1	9.7 1
Gallicolumba longitarsus New Caledonia (U) NCP 100	51.6 1	7.8 1	2.8 2.6–2.9 2	2.1 2.0–2.2 2	7.6 7.6–7.7 2
Gallicolumba stairii Samoa, exact island unknown (M)	30.8 1	6.1 1	2.3 1	1.6 1	5.9 1
Gallicolumba stairii Viti Levu and Rambi, Fiji (2M)	34.0 33.6–34.5 2	6.4 6.4 2	2.6 2.6 2	1.7 1.6–1.8 2	6.4 6.3–6.4 2
Gallicolumba stairii Captive (M)	34.2 1	6.6 1	2.7 1	1.7 1	6.6 1
Gallicolumba stairii Ofu, Samoa (F)	31.8 1	6.2 1	3.0 1	1.8 1	6.7 1
Gallicolumba stairii That Cave, Eua, Tonga (2U) UWBM 862, 1264	30.4 1	— 	2.5 1	1.7 1	—
Gallicolumba stairii Viti Levu and Rambi, Fiji (2F)	31.8 31.7–31.8 2	5.6 5.6–5.7 2	2.6 2.6–2.7 2	1.7 1.7 2	6.3 6.2–6.4 2
Gallicolumba erythroptera Vanavana, Tuamotu Is. (2M)	34.2 33.2–35.1 2	6.4 6.1–6.7 2	2.6 2.5–2.6 2	1.8 1.7–1.8 2	7.2 7.1–7.2 2
Gallicolumba erythroptera Vanavana, Tuamotu Is. (F)	32.8 1	6.3 1	2.3 1	1.7 1	6.9 1
Gallicolumba erythroptera Maria, Tuamotu Is. (M)	34.0 1	6.1 1	2.7 1	1.8 1	7.2 1
Gallicolumba erythroptera Maria, Tuamotu Is. (F)	32.0 31.8–32.2 2	6.2 6.1–6.3 2	2.4 2.4–2.5 2	1.8 1.8 2	6.8 6.6–6.9 2
Gallicolumba erythroptera Te Rua Rere Cave, Mangaia, Cook Is. (3U) USNM 416654–416656	35.9 35.2–37.2 3	6.8 6.7–6.9 3	2.7 2.6–2.8 3	1.8 1.7–1.9 2	6.9 6.9–7.0 3
Gallicolumba sp. unknown Henderson Is. (U) USNM 388744	— 	— 	ca. 3.4 1	— 	—
Gallicolumba rubescens Hatutu, Marquesas (2M)	28.1 27.2–29.0 2	5.2 5.0–5.4 2	2.1 2.1 2	1.4 1.4–1.5 2	5.8 1
Gallicolumba rubescens Hatutu, Marquesas (2F)	26.0 25.2–26.9 2	4.9 4.7–5.1 2	2.0 1.9–2.0 2	1.4 1.3–1.4 2	5.2 4.9–5.6 2
Gallicolumba rubescens Hane Site, Ua Huka, Marquesas (37U) BPBM 162585–162587, 162740, 162741, 163283, 163202, 163313, 168895, 169519, 170297, 170299, 171870, 172058, 173497, 173498, 173500, 173501, 173505, 173525, 173536, 173671, 174443, 175092, 175095, 175097, 175098, 175100, 175102, 176001, 176285, 176289, 180363, 180367, 180372, 180375, 180495	30.1 28.7–31.6 7	5.4 5.0–5.6 14	2.2 2.0–2.5 24	1.5 1.2–1.8 27	5.5 5.2–5.9 14

Table 2. Continued.

	Total length	Proximal width	Least width of shaft	Least depth of shaft	Distal width
Gallicolumba xanthonura Guam, Mariana Is. (1M, 1F)	31.6	6.0	2.6	1.7	6.1
	31.2–32.1	5.9–6.0	2.3–2.8	1.6–1.8	5.8–6.4
	2	2	2	2	2
Gallicolumba luzonica Captive (5M, 5F, 2U) [Philippines]	37.3	6.0	2.6	1.7	6.3
	34.6–40.3	5.6–6.5	2.3–2.7	1.5–1.9	5.9–6.8
	12	12	12	12	12
Gallicolumba criniger Captive (2F) [Philippines]	35.8	6.4	2.6	1.7	6.6
	35.6–35.9	6.4–6.5	2.4–2.8	1.7	6.5–6.6
	2	2	2	2	2
Gallicolumba rufigula New Guinea (F)	35.1	5.3	2.1	1.3	5.5
	1	1	1	1	1
Gallicolumba rufigula Captive (U) [New Guinea]	31.3	5.6	2.4	1.5	5.5
	1	1	1	1	1
Gallicolumba tristigmata Sulawesi, Indonesia (M)	42.1	7.0	2.7	1.7	7.5
	1	1	1	1	1
Gallicolumba tristigmata Sulawesi, Indonesia (F)	47.1	7.1	2.8	2.0	7.6
	1	1	1	1	1
Gallicolumba beccarii New Guinea (3M)	29.6	4.5	1.8	1.2	4.8
	29.0–30.2	4.3–4.7	1.7–1.9	1.1–1.2	4.6–5.0
	2	3	3	3	3
Gallicolumba jobiensis New Guinea (U)	29.5	5.4	2.6	1.8	5.4
	1	1	1	1	1

Ulna. In cranial aspect, the notch between olecranon and cotyla dorsalis larger; papillae remigiales caudales larger; shaft more compressed craniocaudally; tuberculum carpale oriented more perpendicularly (less obtusely) with plane of shaft.

Radius. In proximal aspect, caput radii more rounded (less oblong); shaft narrow relative to caput humeri in lateral aspect; distoventral portion of shaft more rounded.

Carpometacarpus. Foramen in fovea carpalis cranialis larger; fossa supratrochlearis deeper and extends more into cranial side of os metacarpal minus; os metacarpal narrower in ventral aspect.

Phalanx digitalis majoris I. Overall shape more elongate; dorsocaudal and ventrocaudal margins more rounded.

Femur. Facies articularis small in all aspects; crista trochanteris large; corpus femoralis broad in proximal portion but narrow at midpoint.

Tibiotarsus (Table 3; Fig. 3). Crista cnemialis lateralis large; pons supratendineus stout; condylus medialis and condylus lateralis narrow and elongate; mediodistal depth great.

REMARKS. *Gallicolumba nui* is the species listed as "*Gallicolumba* new sp. 2" in Steadman (1989:table 2). At the time that table was compiled, the single furcula of *G. nui* from Tahuata was unrecognized as such. Balouet and Olson (1989:16, 17) described the extinct *Gallicolumba longitarsus* from Holocene deposits on New Caledonia. Except in overall length, the tarsometatarsus of *G. nui* differs substantially in measurements and osteological characters from that of *G. longitarsus* (see Tables 2 and 3 and Diagnosis). Lysaght (1959:278, 303–05, 334) and Balouet and Olson (1989:17) discuss various extinct species and subspecies of *Gallicolumba* from the western Pacific, which include ?*G. norfolcensis* (Latham 1801) of Norfolk Island, Australia, and *G. ferruginea* (Forster 1844) of Tanna Island, Vanuatu [*contra* footnote by E. Mayr in Peters (1937:136)], both of which are much smaller than *G. nui*.

Genus *Macropygia* Swainson 1837

The holotype and paratype tarsometatarsi and tibiotarsi (listed, among other elements, in Table 4) are referred to the genus *Macropygia* rather than to the other genera of columbids in Oceania (*Columba, Ducula, Ptilinopus, Didunculus, Chalcophaps, Gallicolumba,* and *Caloenas*) because of the following unique combination of characters, which are presented in Tables 5 and 6.

Tarsometatarsus: Depth of infracotylaris dorsalis shallow to intermediate; foramina vascularia proximalia absent to medium sized, asymmetrical; shaft stout; fossa metatarsi I placed proximally to intermediately on shaft; foramen vasculare distale small; great amount of plantar rotation of medial trochlea; middle trochlea long to intermediate in length; lateral trochlea significantly rotated laterally; inner trochlea long to intermediate in length.

Tibiotarsus: Great distance between pons supratendineus and papilla on mediodistal part of shaft; junction of shaft with condylus lateralis gradual (obtuse) to intermediate; central papilla in depressio epicondylaris lateralis absent to small; canalis extensorius located medially relative to condyles; proximal half of shaft greatly convex.

Macropygia heana new species

Figures 4, 5; Tables 4–6

HOLOTYPE. BPBM 162574, tarsometatarsus lacking crista hypotarsi.

DIAGNOSIS. A large species of *Macropygia* (Tables 7, 8),

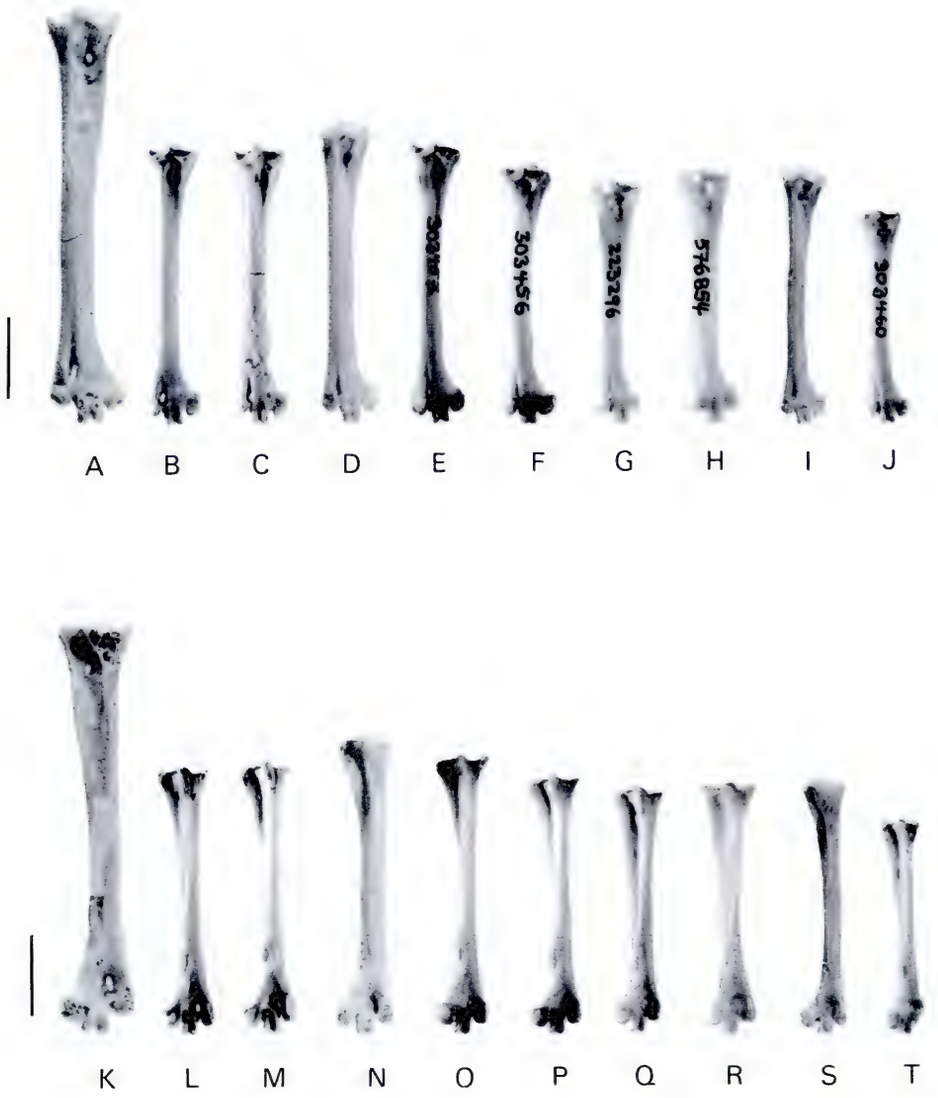

Figure 2. The tarsometatarsus of Polynesian species of *Gallicolumba* in dorsal (**A–J**) and plantar (**K–T**) aspects. **A, K.** *G. nui* n. sp., holotype, unsexed, Hane Site, Ua Huka, Marquesas Islands, BPBM 176000. **B, L.** *G. erythroptera,* unsexed, Te Rua Rere Cave, Mangaia, Cook Islands, USNM 416655. **C, M.** *G. erythroptera,* unsexed, Te Rua Rere Cave, Mangaia, Cook Islands, USNM 416654. **D, N.** *G. erythroptera,* unsexed, Te Rua Rere Cave, Mangaia, Cook Islands, USNM 416656. **E, O.** *G. erythroptera,* male, Vanavana, Tuamotu Islands, USNM 303457. **F, P.** *G. erythroptera,* female, Maria, Tuamotu Islands, USNM 303456. **G, Q.** *G. stairii,* female, Ofu, Samoa, USNM 576854. **H, R.** *G. stairii,* male, Samoa (exact island unknown), USNM 223296. **I, S.** *G. rubescens,* unsexed, Hane Site, Ua Huka, Marquesas Islands, BPBM 176001. **J, T.** *G. rubescens,* male, Hatutu, Marquesas Islands, USNM 303460. The image is reversed in A, C, I, K, M, and S. Scale bar = 10 mm.

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Figure 3. The tibiotarsus of Polynesian species of *Gallicolumba* in cranial (**A–K**) and caudal (**L–V**) aspects. **A, L.** *G. nui* n. sp., paratype, unsexed, Hanatekua Shelter No. 2 Site, Hiva Oa, Marquesas Islands, BPBM 167237. **B, M.** *G. nui* paratype, unsexed, Hane site, Ua Huka, Marquesas Islands, BPBM 173900. **C, N.** *G. erythroptera,* unsexed, Te Rua Rere Cave, Mangaia, Cook Islands, USNM 416656. **D, O.** *G. erythroptera,* unsexed, Te Rua Rere Cave, Mangaia, Cook Islands, USNM 416660. **E, P.** *G. erythroptera,* male, Vanavana, Tuamotu Islands, USNM 303457. **F, Q.** *G. erythroptera,* female, Maria, Tuamotu Islands, USNM 303456. **G, R.** *G. stairii,* female, Ofu, Samoa, USNM 576854. **H, S.** *G. stairii,* male, Samoa (exact island unknown), USNM 223296. **I, T.** *G. rubescens,* unsexed, Hane Site, Ua Huka, Marquesas Islands, BPBM 173437. **J, U.** *G. rubescens,* male, Hatutu, Marquesas Islands, USNM 303460. **K, V.** *G. rubescens,* female, Hatutu, Marquesas Islands, USNM 303459. The image is reversed in D and O. Scale bar = 10 mm.

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Table 3. Measurements (mm) of the tibiotarsus of *Gallicolumba* spp., with mean, range, and sample size. Abbreviations: F, female; M, male; U, sex unknown. Specimen numbers are given for archeological specimens only.

	Total length	Length from crista fibularis	Proximal width	Midshaft width	Midshaft depth	Distal width	Depth of condylus medialis	Depth of condylus lateralis
Gallicolumba nui Hane Site, Ua Huka, Marquesas (17U) BPBM	—	56.0	9.1	4.0	3.5	8.1	8.9	8.0
162530, 162532, 162535, 162600–162602, 169067, 169799, 173175,		55.6–56.3	1	3.8–4.2	3.3–3.8	7.6–8.4	8.3–9.4	7.9–8.0
173539, 173900, 174444, 174445, 176272, 176274, 176629, 176982		2		11	10	9	5	3
Gallicolumba nui Hanatekua Shelter No. 2, Hiva Oa, Marquesas (7U)	86.3	58.0	9.0	4.2	3.9	8.2	9.2	8.0
BPBM 165661, 167237, 167243, 167257, 167281, 167347, 167348	1	1	1	3.9–4.5	3.6–4.0	8.1–8.4	8.8–9.6	7.8–8.2
				5	4	2	2	2
Gallicolumba stairii Rambi and Viti Levu, Fiji (2M)	—	38.6	—	2.5	2.4	5.5	6.0	5.3
		38.4–38.7		2.4–2.6	2.4	5.4–5.6	6.0	5.2–5.4
		2		2	2	2	2	2
Gallicolumba stairii Samoa, exact island unknown (M)	—	—	—	2.3	2.3	5.2	5.2	4.3
				1	1	1	1	1
Gallicolumba stairii Captive (M)	54.0	—	6.2	2.8	2.5	5.6	6.1	5.3
	1		1	1	1	1	1	1
Gallicolumba stairii Rambi and Viti Levu, Fiji (2F)	—	36.2	—	2.5	2.4	5.2	5.8	5.0
		1		2.5	2.4–2.5	5.2	5.7–5.8	4.9–5.0
				2	2	2	2	2
Gallicolumba stairii Ofu, Samoa (F)	53.7	38.3	—	2.9	2.4	5.7	5.9	5.2
	1	1		1	1	1	1	1
Gallicolumba stairii 'Anatu, Eua, Tonga (U) UWBM 695	—	—	—	2.4	2.5	4.8	4.5	4.4
				1	1	1	1	1
Gallicolumba erythroptera Vanavana, Tuamotu Is. (2M)	—	39.5	—	2.4	2.0	5.3	6.0	4.9
		1		2.4–2.5	2.0–2.1	5.3	5.8–6.2	4.8–5.0
				2	2	2	2	2
Gallicolumba erythroptera Maria, Tuamotu Is. (M)	—	37.6	—	2.4	2.1	5.5	5.8	4.8
		1		1	1	1	1	1
Gallicolumba erythroptera Vanavana, Tuamotu Is. (F)	—	37.8	—	2.2	2.0	5.2	5.7	4.7
		1		1	1	1	1	1
Gallicolumba erythroptera Maria, Tuamotu Is. (F)	—	—	—	2.3	2.0	5.3	5.8	4.7
				1	1	5.2–5.4	5.8	4.7
						2	2	2
Gallicolumba erythroptera Te Rua Rere Cave, Mangaia, Cook Is. (3U)	47.8	31.7	5.6	2.7	2.7	5.6	6.5	5.6
USNM 416656, 416659, 416660	1	1	5.3–6.0	2.4–2.8	2.5–2.9	5.4–5.8	1	1
			2	3	3	2		
Gallicolumba rubescens Hatutu, Marquesas (2M)	—	30.3	—	2.0	1.8	4.4	4.8	4.0
		1		2.0–2.1	1.8–1.9	4.4	4.7–5.0	3.8–4.2
				2	2	2	2	2
Gallicolumba rubescens Hatutu, Marquesas (2F)	—	29.7	—	2.0	1.8	4.2	4.6	3.8
		1		2.0	1.6–1.9	4.0–4.4	4.3–4.8	3.6–4.0
				2	2	2	2	2

Table 3. Continued.

	Total length	Length from crista fibularis	Proximal width	Midshaft width	Midshaft depth	Distal width	Depth of condylus medialis	Depth of condylus lateralis
Gallicolumba rubescens Hane Site, Ua Huka, Marquesas (63U) BPBM 162561, 162565, 162569, 162572, 162697, 162707, 162728, 162729, 162780, 162783, 163148, 163163, 163207, 163272, 163274, 168929, 168933, 168942, 169095, 169147, 169148, 170231–170233, 170236, 170241, 170611, 170827, 170994, 171313, 171379–171382, 171385, 171926, 172208, 173436, 173437, 173448, 173460, 173468, 173476, 173655, 173772, 175001, 175080, 175083, 175084, 175086, 175140, 175153, 175154, 175397, 176711, 176991, 180529, 180535, 180289, 180536, 180539, 180547, 180551	46.3 45.2–47.4 3	33.5 32.4–34.6 3	4.5 4.3–4.8 5	2.1 1.9–2.3 37	1.9 1.7–2.1 37	4.6 4.2–5.1 29	5.0 4.6–5.3 19	4.1 3.7–4.5 16
Gallicolumba rubescens Hanamiai Site, Tahuata, Marquesas (3U) BPBM 166794, 166796, 166801	—	—	—	2.1 1	1.9 1	4.8 4.6–4.9 2	5.1 4.9–5.3 2	4.1 1
Gallicolumba xanthonura Guam, Mariana Is. (1M, 1F)	52.0 51.5–52.6 2	37.9 36.8–39.0 2	5.1 1	2.4 2.2–2.5 2	2.3 2.2–2.4 2	5.2 5.2 2	5.5 5.5 2	4.8 4.8 2
Gallicolumba luzonica Captive (9M, 4F, 2U)	56.0 53.3–61.5 14	39.2 37.7–42.2 12	5.5 5.1–5.7 6	2.7 2.4–3.1 15	2.5 2.3–2.8 15	5.4 4.8–6.0 14	5.8 5.5–6.2 13	5.0 4.7–5.6 15
Gallicolumba criniger Captive (F)	54.4 1	—	5.5 1	2.6 1	2.2 1	5.5 1	5.5 1	5.0 1
Gallicolumba rufigula New Guinea (F)	53.1 1	37.1 1	4.7 1	2.2 1	1.9 1	4.8 1	5.2 1	4.6 1
Gallicolumba rufigula Captive (U)	49.0 1	—	5.0 1	2.2 1	2.1 1	4.6 1	5.0 1	4.4 1
Gallicolumba tristigmata Sulawesi, Indonesia (M)	66.6 1	46.7 1	6.6 1	3.1 1	2.9 1	6.1 1	6.6 1	5.9 1
Gallicolumba tristigmata Sulawesi, Indonesia (F)	67.7 1	50.4 1	6.5 1	3.2 1	2.9 1	6.4 1	6.9 1	6.2 1
Gallicolumba beccarii New Guinea (3M)	45.2 44.9–45.8 3	33.4 33.2–33.7 2	3.9 3.8–4.0 3	1.8 1.7–1.9 3	1.7 1.7–1.8 3	3.8 3.6–4.0 3	4.1 3.8–4.3 3	3.6 3.5–3.8 3
Gallicolumba jobiensis New Guinea (U)	49.2 1	—	5.0 1	2.6 1	2.4 1	5.0 1	5.3 1	4.7 1

Table 4. **Bones of *Macropygia heana* new species, by element. All specimens are from the Hane Archeological Site, Ua Huka, Marquesas Islands. Numbers refer to the number of identified specimens (NISP).**

Quadrate	1
Rostrum	1
Mandible	1
Sternum	7
Coracoid	41
Scapula	12
Humerus	12
Ulna	17
Radius	4
Carpometacarpus	10
Phalanx digitalis majoris I	1
Femur	15
Tibiotarsus	37
Tarsometatarsus	39
Pedal phalanx	1
Total	199

further distinguished from congeners as follows: tarsometatarsus—more slender overall, inner trochlea relatively longer, foramina vascularia proximalia very small or absent; tibiotarsus—shaft more slender relative to total length, tuberositas retinaculi musculo fibularis much reduced or absent, central papilla in depressio epicondylaris lateralis absent (present in *M. amboinensis* and *M. phasianella*). The tibiotarsus of the newly described species from Huahine (see later) agrees with that of *M. heana* in the first two characters just stated but differs in the third character, in size (Table 8), and in having a more abrupt (less obtuse) junction of the shaft and condylus lateralis.

TYPE LOCALITY AND HORIZON. Hane Site, MUH-1 (also known as "Hane Dune Site"), Ua Huka, Marquesas Islands (Fig. 3), Layer IV, Area A, collected in 1964–1965 by Yosihiko H. Sinoto and associates.

TOPOTYPICAL PARATYPES. Rostrum, BPBM 174014, quadrate, BPBM 173647; mandible, BPBM 176956; 7 sterna, BPBM 163336, 171970, 173632, 180392, 180394, 180395, 181304; 41 coracoids, BPBM 162540, 162544, 162659, 162662, 162667, 163252, 163254–163256, 163263, 163338, 163363–163365, 165535, 165586, 168880, 168883, 168990, 168991, 169121, 169123, 169165, 169533, 169538, 170266, 171888, 173601, 173603, 173604, 173608, 173609, 173611, 173613, 173614, 173742, 174141, 174424, 176014, 176267, 176495; 12 scapulae, BPBM 162673, 163366, 163367, 169520, 169557, 171414, 173540–173542, 175338, 176295, 180386; 12 humeri, BPBM 163257, 163323, 163324, 171121, 171189, 173620–173623, 174450, 176015, 176056, 180291; 17 ulnae, BPBM 162612, 162613, 162619, 162620, 162946–162948, 169512, 170279–170281, 173562–173564, 173567, 173805, 180324; 4 radii, BPBM 162614, 163454, 173808, 176038; 10 carpometacarpi, BPBM 162949–162951, 163305, 163368, 168989, 170683, 171886, 172016, 176062; phalanx digitalis majoris I, BPBM 162955; 15 femora, BPBM 162618, 162778, 163211, 164885, 168996, 169506, 169522, 170270, 171889, 173418, 173421, 176010, 176011, 180287, 180507; 37 tibiotarsi, BPBM 162566, 162567, 162696, 162706, 162713, 163236, 163276, 163308, 168938, 168953, 169491, 169531, 169539, 170246, 170247, 170255, 170614, 171319, 173444, 173457, 173467, 173471, 173481, 173486, 173654, 173938, 174416, 174418, 175089, 175155, 176019, 176023, 176026, 176032, 176279, 181288, 181290; 39 tarsometatarsi, BPBM 162573, 162574, 162626, 163001, 163005, 163280, 163332, 163335, 168906, 169104, 169501, 169504, 169549, 170152, 170160, 170169, 170173, 170351, 171404, 171409, 171410, 171869, 173512, 173520, 173524, 173526, 173529, 173532, 173743, 173812, 173881, 176047, 176048, 176050, 176051, 176053, 180374, 180377, 181292–181294; pedal phalanx, BPBM 173809.

ETYMOLOGY. From the Marquesan word *heana*, which means "victim" (Dening, 1980:55, 248–49). A Marquesan tradition, which died out in the nineteenth century, was to avenge a death by capturing, usually killing, and sometimes eating, another person known as the *heana*. Regardless of whether the loss of *Macropygia heana* was primarily a result of habitat alteration or predation by humans and introduced mammals, this extinct cuckoo-dove was a victim of the arrival of people in the Marquesas Islands.

DESCRIPTION. The elements of *Macropygia heana* other than the tarsometatarsus and tibiotarsus, listed earlier, are referred to *M. heana* in part because of their unique intermediate size among Marquesan columbids [smaller than *Ducula galeata* (Bonaparte 1855) or *Gallicolumba nui*, but larger than *Gallicolumba rubescens*, *Ptilinopus dupetithouarsii* (Neboux 1840), or *P. mercierii* (Des Murs and Prévost 1849)]. These referrals are supported further by having a wing–leg elemental ratio more similar to those of modern species of *Macropygia* and *Ducula* than to those of *Ptilinopus* or *Gallicolumba* (Table 9) and by having these characters of *Macropygia* rather than of *Columba*, *Ducula*, *Ptilinopus*, *Chalcophaps*, *Gallicolumba*, *Didunculus*, or *Caloenas:* coracoid—processus acrocoracoideus protrudes more dorsad than in *Ducula* or *Ptilinopus*, impressio musculo sternocoracoideus lacks distinct depression on medial side (present in all others); scapula—facies articularis humeralis more protrudent from shaft than in *Ducula*, cranial margin of facies articularis humeralis more pointed than in *Ducula* or *Ptilinopus;* humerus—more slender overall than in *Columba*, *Chalcophaps*, or *Caloenas;* ulna—papillae remigiales caudales smaller than in *Columba*, *Chalcophaps*, *Gallicolumba*, *Didunculus*, or *Caloenas;* carpometacarpus—more slender overall than in *Columba*, *Chalcophaps*, or *Caloenas*.

Macropygia arevarevauupa new species

Figure 5; Tables 6, 8

HOLOTYPE. DAPT 135, tibiotarsus lacking only condylus medialis.

TYPE LOCALITY AND HORIZON. Fa'ahia Site (ScH 1-2), Huahine Society Islands (Fig. 7), square R43–44 (sump), collected in 1985 by Yosihiko H. Sinoto and associates.

DIAGNOSIS. A species of *Macropygia* that differs from congeners as follows: very large size (Table 8); junction of shaft with condylus lateralis is more abrupt (less obtuse) than in all except *M. phasianella;* central papilla in depressio epicondylaris lateralis present (absent in *M. heana*, *M. unchall*, and *M. nigrirostris*). Specific differences between the tibiotarsus of *M. arevarevauupa* and that of the newly described *M. heana* (its only Polynesian congener) are listed in the Diagnosis of *M. heana*.

ETYMOLOGY. From the Tahitian words *arevareva*, meaning "cuckoo" (*Eudynamis taitensis* Sparrman 1787), and *u'upa*, meaning "dove" (*Ptilinopus purpuratus* Gmelin 1789) (London Missionary Society, 1851:37, 306; Thibault and Rives, 1975:90, 92). Thus, the name *arevarevauupa* is a Tahitian (=Society Is-

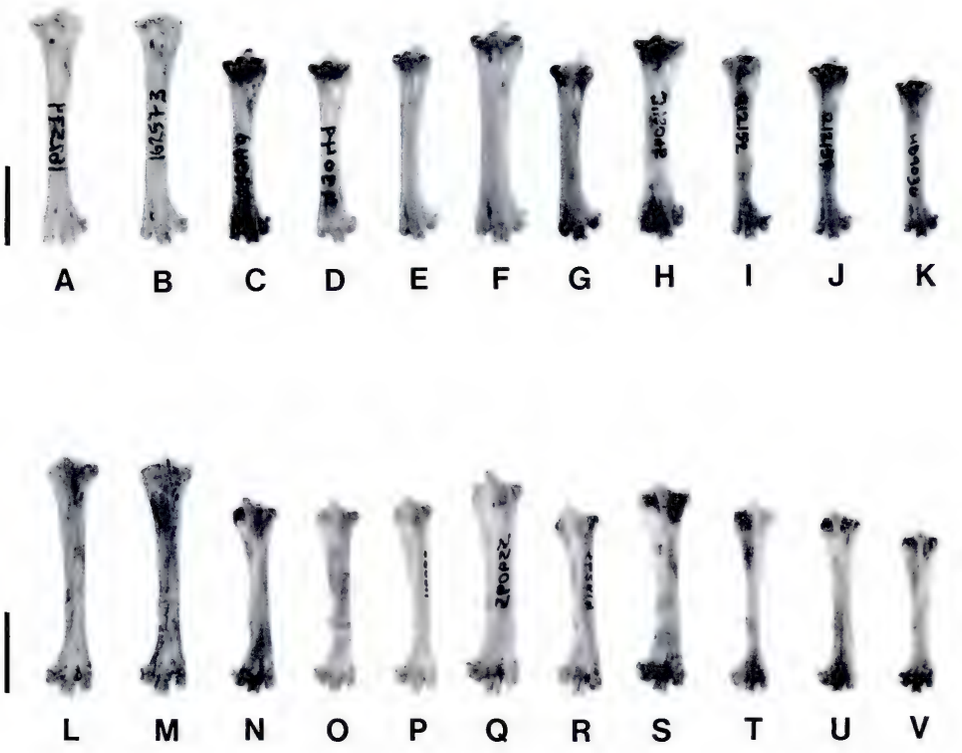

Figure 4. The tarsometatarsus of *Macropygia* in dorsal (**A–K**) and plantar (**L–V**) aspects. **A, L.** *M. heana* n. sp., holotype, unsexed, Hane Site, Ua Huka, Marquesas Islands, BPBM 162574. **B, M.** *M. heana* n. sp., paratype, unsexed, Hane Site, Marquesas Islands, BPBM 162573. **C, N.** *M. amboinensis,* male, New Guinea, UWBM 43048. **D, O.** *M. amboinensis,* female, New Guinea, UWBM 43049. **E, P.** *M. amboinensis,* male, Halmahera, Northern Moluccas, USNM 558311. **F, Q.** *M. phasianella* (*phaea*?), male, Sabtang Island, Philippines, USNM 560655. **G, R.** *M. phasianella tenuirostris,* female, Negros Island, Philippines, USNM 562814. **H, S.** *M. unchall,* male, Thailand, USNM 343045. **I, T.** *M. mackinlayi,* male, Epi, Vanuatu, AMNH 212152. **J, U.** *M. mackinlayi,* female, Epi, Vanuatu, AMNH 212159. **K, V.** *M. nigrirostris nigrirostris,* male, New Guinea, USNM 489036. Image is reversed in A, C–H, L, and N–S. Scale bar = 10 mm.

land) translation of the English name most commonly used for living species of *Macropygia.*

REMARKS. *Macropygia heana* is the undescribed species listed as "*Gallicolumba* new sp. 1" in Steadman (1989:table 2). At the time that table was compiled, the existence of *Macropygia* in East Polynesia was unrecognized and unsuspected. The record on Tahuata for "*Gallicolumba* new sp. 1" in Steadman (1989:table 2) has been invalidated, the specimens instead representing an extirpated population of *G. rubescens.*

Macropygia heana and *M. arevarevauupa* probably are more closely related to each other than to any other species, both having relatively long, slender legs. Modern skeletons are not available for *M. ruficeps* (Temminck 1834), a very small species from Southeast Asia and Indonesia, and two larger species that are closely related to *M. phasianella: M. rufipennis* Blyth 1846, endemic to the Andaman and Nicobar islands, Indian Ocean (Ripley and Beehler, 1989), and *M. magna* Wallace 1863, of Indonesian islands southeast of Sulawesi (Mayr, 1944:133, 148–49, 191). The species-level systematics of the larger species of *Macropygia,* especially of *M. amboinensis* and *M. phasianella,* are uncertain and difficult to resolve (Mayr, 1944:148–49; Goodwin, 1967:147, 148; Frith, 1982:144).

The holotype of *Macropygia arevarevauupa* is larger than the tibiotarsus of any other species of *Macropygia.* It is most closely approached in size by *Reinwardtoena reinwardtii,* from which it differs in being much more slender overall and in having a more rounded cranial surface of condylus lateralis. Skeletal measurements of modern specimens (Tables 7, 8) reveal no difference in the size of males versus females in any species of *Macropygia,* thus reducing the possibility that even a portion of the difference in size between *M. arevarevauupa* and *M. heana* could be due to sexual dimorphism. In standard measurements of skins from Australia (wing, tail, tarsus, exposed culmen, total culmen), Frith (1982:144) found males of *M. phasianella* to average slightly larger than females, with much overlap.

DISCUSSION

EXTINCTION

Archeological sites from East Polynesia have yielded thousands of bones of seabirds and landbirds. Although the bones of landbirds are rarer than those of seabirds, they include a greater percentage of extinct species. The extinct landbirds are dominated by rails, pigeons, parrots, and passerines (Steadman, 1985, 1987, 1988, 1989; Steadman and Olson, 1985; Steadman and Zarriello, 1987; Dye and Steadman, 1990). On islands where rich archeological faunas have been recovered, such as Ua Huka, Hiva Oa, Tahuata, Huahine, and Mangaia, the prehistoric landbird fauna consists of three to four times more species than the modern fauna (Steadman, 1989) and, thus, approaches the very high levels of late Quaternary extinction seen in the Hawaiian Islands (James et al., 1987).

Table 5. Characters of the tarsometatarsus of various species of *Macropygia* versus other genera of columbids from Oceania. Abbreviations: AB, absent; AS, asymmetrical; E, elongate; I, intermediate; L, large; S, small; SY, symmetrical.

	Fossa infracotylaris dorsalis	Foramina vascularia proximalia	Overall stoutness of shaft	Relative placement of fossa metatarsi I
Macropygia heana	shallow	very S; AS; often 1 AB	stout	I
Macropygia amboinensis	shallow	S-I; AS	stout	proximal
Macropygia phasianella	I	S-I; AS	stout	I
Macropygia unchall	shallow	S-I; AS; often 1 AB	stout	proximal
Macropygia mackinlayi	I	S; AS	stout	I
Macropygia nigrirostris	shallow	S; AS	stout	I
Reinwardtoena (reinwardtii)	I	S; AS	stout	proximal
Columba (vitiensis)	deep	L; AS	stout	I
Ducula (pacifica)	deep	L; AS	stout	proximal
Ptilinopus (dupetithouarsii)	deep	L; AS	I	proximal
Gallicolumba (rubescens)	S-I	S; SY	slender	distal
Didunculus (strigirostris)	deep	L; AS	slender	distal
Chalcophaps (indica)	I	S; AS; often 1 AB	I	distal
Caloenas (nicobarica)	I	L; AS; often 1 AB	I	distal

Gallicolumba nui is only the second extinct species of *Gallicolumba* to be described from bones, the other being *G. longitarsus* of New Caledonia (Balouet and Olson, 1989). *Macropygia heana* and *M. arevarevauupa* are the first extinct species of *Macropygia* to be described. The archeological strata on Ua Huka and Hiva Oa that bear bones of *G. nui* and *M. heana* are from 2,000 to 1,000 years old and represent the earliest known phases of Marquesan culture (Sinoto, 1966, 1968, 1979; Bellwood, 1972, 1979; Kirch, 1986). Strata from the Hanamiai Site on Tahuata bearing bones of *G. nui* appear to be about 1,000–800 years old (Rolett, 1989). On all three of these Marquesan islands, the archeological strata less than 800 years old have not yielded a single bone of *G. nui* or *M. heana*. The Fa'ahia Site on Huahine, which has yielded bones of *G. nui* and *M. arevarevauupa*, dates to about 1,250–750 B.P. (Sinoto, 1979, 1983; Sinoto and McCoy, 1975; Emory, 1979; Pigeot, 1985, 1986). The bones of *G. nui* from Te Rua Rere Cave and Tuatini Cave on Mangaia are undated other than probably being cultural in origin, thereby suggesting ages of less than 1,500–2,000 years old (Steadman, 1985, 1987, 1989). The bones of *G. nui* from Tangatatau Rockshelter on Mangaia are from archeological strata dated at about 1,000–700 B.P. (Steadman and Kirch, 1990). These bones are associated with bones of other animals eaten by prehistoric Mangaians, such as rats [*Rattus exulans* (Peale 1848)], pigs (*Sus scrofa* Linnaeus 1758), fruit bats (*Pteropus tonganus* Quoy and Gaimard 1830), more than 20 other species of birds, and a variety of fish.

The lack of specimens or written records of *Gallicolumba nui, Macropygia heana,* or *M. arevarevauupa* during the past 200 years, and the lack of their bones from archeological strata less than about 700 years old, suggest that these species died out before the period of European contact. Had *G. nui* survived into European times, which seems doubtful, predation by feral cats (*Felis cattus* Linnaeus 1758) probably would have destroyed any remaining individuals. On Rennell in the Solomon Islands, for example, introduced cats seem to have depleted the formerly common and widespread *G. beccarii* within a few decades (Diamond, 1984:153). Because the bones of all three species described herein are from the context of kitchen middens, they undoubtedly were hunted and eaten by prehistoric peoples. By foraging exclusively or mainly on the ground, species of *Gallicolumba* probably were (and still are, where they survive) particularly vulnerable to predation from human-set snares and the rats (*Rattus exulans*), dogs (*Canis familiaris* Linnaeus 1758), and perhaps pigs (*Sus scrofa*) that arrived with Polynesians.

The slightly lower wing–leg ratio of *Macropygia heana* might suggest a somewhat more sedentary or terrestrial existence than in modern species of *Macropygia* (Table 9). Tameness could have been another factor contributing to the extinction. In Australia, *M. phasianella* "is tamer than other rainforest pigeons and, if disturbed while in a low tree, it usually remains there. When disturbed from low bushes, it flits only a short distance to a low tree where it watches the observer and returns when he has gone" (Frith, 1982:145). Similar behavior by *M. heana* and *M. arevarevauupa* would have been to the liking of early Polynesian hunters. Evolving in the absence of mammalian predators, the insular species probably were even tamer than *M. phasianella*.

Like surviving species of *Gallicolumba, G. nui* probably nested on or near the ground rather than in trees, thus making it particularly vulnerable to introduced mammalian predators. In Papua New Guinea today, *G. rufigula* and *G. beccarii* build nests only 0.9–2.7 m and 0–3 m above the ground, respectively (Coates, 1985:284–85, 287). Perhaps the nesting habits of the two extinct species of *Macropygia* contributed to their vulnerability as well. Today, *M. amboinensis* builds a relatively "large and bulky" nest only 0.9–4.6 m above the ground in Papua New Guinea (Coates, 1985:263), although *M. phasianella* in Australia builds a nest that varies greatly in size and location (Frith, 1982: 148).

Habitat alteration, particularly the clearing of forests for agriculture and habitation sites, probably was another important factor in the extinction of all three newly described species, whose congeners all inhabit forests. Even the species of *Macropygia* that occur in second-growth forests seem to require the nearby presence of some primary forest.

BIOGEOGRAPHY

Meaningful evolutionary or biogeographic analyses depend upon accurate information on the ranges of individual species. Because

Table 5. Continued.

Foramen vascular distale	Plantar rotation of inner trochlea	Relative length of middle trochlea	Plantar rotation of lateral trochlea	Relative length of inner trochlea
S	great	long	yes	long
S	great	long	yes	I
S	great	I	yes	I
S	great	long	yes	I
S	great	I	yes	I
S	great	long	yes	I
S	great	long	yes	I
S	great	long	yes	short
L; E	slight	long	very slight	long
L; E	none	short	no	short
S; E or not E	great	I	yes	short
S	great	long	yes	I
S	great	I	yes	short
S	great	long	yes	short

the natural ranges of virtually all species of Polynesian landbirds have been reduced through human activities of the past several thousand years (Steadman, 1989), reliable estimates of natural ranges are possible only through the study of bones from archeological sites.

As pointed out by Balouet and Olson (1989:17), the spotty ranges of the living species of *Gallicolumba* are a result of human influences rather than natural processes. The ranges of all Polynesian species of *Gallicolumba* have been reduced since human colonization of the islands. *Gallicolumba erythroptera* is known historically only from Tahiti and Mo'orea (Society Islands) and various islands of the Tuamotu Archipelago. It has been extirpated on Tahiti and Mo'orea. Bones of *G. erythroptera* have been identified from archeological sites on Huahine (Society Islands) and Mangaia and Atiu in the Cook Islands (Steadman, 1985, 1989). *Gallicolumba rubescens* is known historically only from the Marquesan islands of Nuku Hiva, Hatutu, and Fatu Huku, being extirpated today on the former. Elsewhere in the Marquesas, I have identified bones of *G. rubescens* from archeological sites on Ua Huka, Hiva Oa, and Tahuata (Steadman,

Table 6. Characters of the tibiotarsus of various species of *Macropygia* versus other genera of columbids from Oceania. Abbreviations: EX, excavated; I, intermediate; SL, slightly.

	Relative distance from pons supratendineus to papilla on medio-distal part of shaft	In lateral aspect, nature of junction of shaft with condylus lateralis	Central papilla in depressio epicondylaris lateralis	Location of canalis extensorius relative to condyles	Convexity of proximal half of shaft
Macropygia heana	great	gradual	absent	medial	great
Macropygia arevarevauupa	great	I	small	medial	great
Macropygia amboinensis	great	gradual	small	medial	great
Macropygia phasianella	great	I	small	medial	great
Macropygia unchall	great	gradual	absent	medial	great
Macropygia mackinlayi	great	I	small	medial	I
Macropygia nigrirostris	great	gradual	absent	medial	great
Reinwardtoena (reinwardtii)	great	gradual	small	medial	great
Columba (vitiensis)	great	abrupt; SL EX	large	medial	great
Ducula (pacifica)	great	abrupt; SL EX	absent	medial	little
Ptilinopus (dupetithouarsii)	great	abrupt; EX	large	centered	little
Gallicolumba (rubescens)	small	I	absent	medial	great
Didunculus (strigirostris)	small	abrupt	absent	medial	little
Chalcophaps (indica)	small	I	small	medial	little
Caloenas (nicobarica)	small	I	absent	medial	little

Figure 5. The tibiotarsus of *Macropygia* in cranial (**A–L**) and caudal (**M–X**) aspects. **A, M.** *M. heana* n. sp., paratype, unsexed, Hane Site, Ua Huka, Marquesas Islands, BPBM 162696. **B, N.** *M. heana* n. sp., paratype, unsexed, Hane Site, Ua Huka, Marquesas Islands, BPBM 162567. **C, O.** *M. arevarevauupa* n. sp., holotype, unsexed, Fa'ahia Site, Huahine, Society Islands, DAPT 135. **D, P.** *M. amboinensis,* male, New Guinea, UWBM 43048. **E, Q.** *M. amboinensis,* female, New Guinea, UWBM 43049. **F, R.** *M. amboinensis,* male, Halmahera, Northern Moluccas, USNM 558311. **G, S.** *M. phasianella* (*phaea*?), male, Sabtang Island, Philippines, USNM 560655. **H, T.** *M. phasianella tenuirostris,* female, Negros Island, Philippines, USNM 562814. **I, U.** *M. unchall,* male, Thailand, USNM 343045. **J, V.** *M. mackinlayi,* male, Epi, Vanuatu, AMNH 212152. **K, W.** *M. mackinlayi,* female, Epi, Vanuatu, AMNH 212159. **L, X.** *M. nigrirostris nigrirostris,* male, New Guinea, USNM 489036. Scale bar = 10 mm.

1989; Table 8 herein). Likewise, the very discontinuous range of *G. stairii* in Fiji, Tonga, Samoa, Wallis, and Futuna (duPont, 1976:71; Watling, 1982:80; Pratt et al., 1987:194–95) is probably a result of human-induced extirpations rather than natural causes, although few islands in this region have been sampled for prehistoric bird bones. An exception is the Tongan island of Eua, where many bones of *G. stairii* have been found in late Pleistocene and Holocene cave deposits, providing the southernmost record for the species (Steadman, 1989).

The range of the extinct *Gallicolumba nui,* which spanned more than 2,000 km of East Polynesia, consisted of Ua Huka and Hiva Oa in the Marquesas Islands, Huahine in the Society Islands, and Mangaia in the Cook Islands (Figs. 6–9). This extremely discontinuous range, which is geographically illogical without including many intervening islands, closely resembles that of another large pigeon, *Ducula galeata* (Steadman, 1989; Steadman and Olson, 1985; Olson and Steadman, 1987). As archeological bones are found elsewhere in East Polynesia (Marquesas, Society, Tuamotu, and Cook Islands), I believe that *G. nui* (and *D. galeata*) will be found to have occurred virtually throughout East Polynesia.

From Henderson Island in the Pitcairn Group, a single, fragmentary tarsometatarsus of *Gallicolumba* sp. has been reported from an archeological site (Schubel and Steadman, 1989). This

Table 7. Measurements (mm) of the tarsometatarsus of *Macropygia* spp., with mean, range, and sample size. Abbreviations: F, female; M, male; U, sex unknown. Specimen numbers are given for archeological specimens only.

	Total length	Proximal width	Least width of shaft	Least depth of shaft	Distal width
Macropygia heana Ua Huka, Marquesas (22U) 162573, 162574, 163001, 163005, 163280, 168906, 169504, 169549, 170160, 170169, 171409, 171410, 173520, 173524, 173532, 176047, 176048, 180374, 180377, 181292–181294	26.6	6.2	2.5	1.8	5.6
	26.0–27.1	6.0–6.4	2.3–2.6	1.8–1.9	5.5–5.9
	4	9	13	17	9
Macropygia amboinensis Halmahera, Northern Moluccas (4M, 7F)	21.2	5.2	2.2	1.6	4.7
	20.0–22.3	5.0–5.4	1.9–2.5	1.4–1.8	4.4–4.8
	11	11	11	11	11
Macropygia amboinensis Obi, Northern Moluccas (M)	22.6	4.9	2.0	1.6	4.7
	1	1	1	1	1
Macropygia amboinensis New Guinea (M, 2F)	21.8	5.3	2.2	1.7	5.1
	21.3–22.3	5.2–5.4	2.1–2.3	1.6–1.8	4.9–5.3
	3	3	3	3	3
Macropygia phasianella [*phaea*?] Batanes Is., Philippines (M)	24.5	6.3	3.1	2.2	6.0
	1	1	1	1	1
Macropygia phasianella tenuirostris Negros Is., Philippines (2F)	21.6	5.6	2.4	1.8	5.2
	21.2–21.9	5.4–5.7	2.3–2.6	1.7–1.9	5.2
	2	2	2	2	2
Macropygia phasianella subsp. Leyte Is., Philippines (F, U)	22.7	5.6	2.6	1.8	5.3
	22.7	5.5–5.7	2.5–2.8	1.8–1.9	5.3
	2	2	2	2	2
Macropygia unchall Thailand (M, F)	23.4	6.1	2.7	2.0	5.6
	23.2–23.7	5.9–6.3	2.6–2.8	1.9–2.0	5.5–5.6
	2	2	2	2	2
Macropygia unchall Captive (4F, U)	22.1	5.8	2.5	1.8	5.2
	21.6–22.4	5.7–6.1	2.4–2.7	1.7–1.9	5.0–5.6
	5	5	5	5	5
Macropygia mackinlayi Epi, Vanuatu (M, F)	21.0	4.8	1.9	1.4	4.6
	20.5–21.4	4.8	1.8–2.0	1.3–1.4	4.4–4.7
	2	2	2	2	2
Macropygia nigrirostris New Guinea (2M)	18.4	4.6	2.0	1.4	4.4
	18.3–18.4	4.4–4.7	1.9–2.0	1.4	4.2–4.5
	2	2	2	2	2
Reinwardtoena reinwardti Halmahera (M)	25.9	6.8	3.0	2.3	6.7
	1	1	1	1	1

specimen (USNM 388744) may represent a new species, but it is too incomplete to provide a basis for formal description. Although USNM 388744 is closer in size to the tarsometatarsus of *G. nui* than *G. erythroptera* (Table 2), it resembles that of *G. erythroptera* rather than *G. nui* in its more smoothly curved, shallower proximomedial margin of the shaft, the presence of a lateral foramen vascularium proximalium, and the shallower fossa infracotylaris dorsalis. Thus, the specimen from Henderson Island, which represents the southeasternmost record for any species of *Gallicolumba,* is a large form that probably is most closely related to *G. erythroptera,* which occurs on islands in the Tuamotu Archipelago no less than 1,000 km from Henderson Island.

Until now, only one species of *Gallicolumba* has ever been recorded on any single Polynesian island. With the discovery of *G. nui,* at least two species of *Gallicolumba* are known to have coexisted on Ua Huka, Hiva Oa, Huahine, and Mangaia. On Ua Huka and Hiva Oa, *G. nui* was sympatric with *G. rubescens* (Table 10). On Huahine and Mangaia, *G. nui* was sympatric with *G. erythroptera.* The sympatry of *G. nui* and *G. rubescens* probably occurred throughout the Marquesas, while that of *G. nui* and *G. erythroptera* probably existed through much of the Tuamotu, Society, and Cook Islands. An expanded record of archeological bones will test these suggestions.

The range of *Macropygia heana* is confined thus far to Ua Huka (Figs. 6, 9). This is probably an artifact of the much smaller sample size of archeological bones available from other islands in the Marquesas. For example, about 1,800 bones of columbids have been recovered from the Hane Site on Ua Huka, compared to only 144 columbid bones from Hiva Oa, 27 from Tahuata, and two from Nuku Hiva. Furthermore, bones of birds the size of or smaller than *M. heana* are extremely scarce in the Hiva Oa collections, reflecting inadequate methods of field recovery.

Like *Macropygia heana, M. arevarevauupa* is known thus far from only one island, although the natural range probably was much greater. Some of the other extinct or extirpated landbirds from the Fa'ahia Site, Huahine, have been found in archeological contexts elsewhere in East Polynesia (Steadman,

Table 8. Measurements (mm) of the tibiotarsus of *Macropygia* spp., with mean, range, and sample size. Abbreviations: F, female; M, male; U, sex unknown. Specimen numbers are given for archeological specimens only.

	Total length	Length from crista fibularis	Midshaft width	Midshaft depth	Distal width	Depth of condylus medialis	Depth of condylus lateralis
Macropygia heana Ua Huka, Marquesas (10U) 163236, 170614, 173444, 173457, 173467, 173481, 173486, 173938, 174416, 175155	—	ca. 33.4	2.2	2.2	5.5	5.3	4.6
		1	2.2–2.3	2.1–2.2	5.2–5.9	4.9–5.6	4.4–4.7
			4	4	7	5	4
Macropygia arevarevauupa Huahine, Society Is. (U) DAPT 135	55.0	39.6	2.9	2.7	—	—	5.5
	1	1	1	1			1
Macropygia amboinensis Halmahera, Northern Moluccas (4M, 7F)	40.9	27.0	2.4	2.0	4.8	4.4	4.0
	39.1–42.2	25.4–28.1	2.2–2.7	1.9–2.1	4.6–5.1	4.2–4.8	3.8–4.4
	11	11	11	11	11	11	11
Macropygia amboinensis Obi, Northern Moluccas (M)	42.1	28.5	2.2	2.0	4.6	4.4	3.9
	1	1	1	1	1	1	1
Macropygia amboinensis New Guinea (M, 2F)	41.5	26.8	2.3	2.0	4.8	4.6	4.2
	40.8–42.1	25.5–27.7	2.2–2.5	1.9–2.0	4.8–4.9	4.5–4.7	4.1–4.3
	3	3	3	3	3	3	3
Macropygia phasianella [*phaea*?] Batanes Is., Philippines (M)	47.8	31.2	3.2	2.5	5.6	5.3	4.9
	1	1	1	1	1	1	1
Macropygia phasianella tenuirostris Negros Is., Philippines (2F)	43.0	26.8	2.6	2.0	5.0	4.8	4.4
	42.2–43.9	26.4–27.2	2.5–2.8	1.9–2.2	4.8–5.2	4.8–4.9	4.3–4.5
	2	2	2	2	2	2	2
Macropygia phasianella subsp. Leyte Is., Philippines (F, U)	43.8	29.4	2.7	2.2	5.2	5.0	4.4
	43.8	29.3–29.6	2.6–2.8	2.2–2.3	5.2	4.8–5.1	4.4
	2	2	2	2	2	2	2
Macropygia unchall Thailand (M, F)	46.6	29.4	3.0	2.6	5.4	5.1	4.6
	46.4–46.8	29.2–29.6	2.9–3.0	2.5–2.6	5.3–5.5	5.0–5.2	4.6–4.7
	2	2	2	2	2	2	2
Macropygia unchall Captive (4F, U)	43.8	27.9	2.6	2.1	5.1	4.8	4.5
	42.4–44.5	27.1–28.6	2.5–2.7	2.0–2.2	5.0–5.4	4.8–4.9	4.2–4.6
	5	5	5	5	5	4	5
Macropygia mackinlayi Epi, Vanuatu (M, F)	—	26.6	1.8	1.6	4.3	4.4	4.0
		1	1.8	1.6–1.7	4.2–4.4	4.3–4.4	3.8–4.1
			2	2	2	2	2
Macropygia nigrirostris New Guinea (2M)	36.4	24.2	2.0	1.8	4.0	3.8	3.6
	36.3–36.6	24.1–24.2	2.0–2.1	1.7–1.8	4.0	3.7–4.0	3.4–3.7
	2	2	2	2	2	2	2
Reinwardtoena reinwardtii Halmahera (M)	49.6	32.9	3.2	2.6	6.1	6.3	5.6
	1	1	1	1	1	1	1

Table 9. Relative lengths (mm) of major distal elements of the wing (carpometacarpus) and leg (tarsometatarsus) in various columbids of Oceania.

	Length of carpometacarpus (C)	Length of tarsometatarsus (T)	C/T
Macropygia heana BPBM 162573, 162574, 162950, 163305, 176047, 180377	28.8 (28.0–29.6) 2	26.6 (26.0–27.1) 4	1.08
Macropygia amboinensis USNM 557039	24.8	21.0	1.18
Macropygia phasianella [*phaea*?] USNM 560655	28.7	24.4	1.18
Macropygia phasianella tenuirostris USNM 562814	26.0	21.2	1.23
Macropygia unchall USNM 343045	29.6	23.5	1.26
Macropygia nigrirostris USNM 489036	20.9	18.3	1.14
Reinwardtoena reinwardtii USNM 560800	33.8	25.8	1.31
Columba vitiensis USNM 561555	36.4	30.1	1.21
Ducula pacifica UWBM 42653	35.2	30.7	1.15
Ducula oceanica UWBM 43008	33.0	32.1	1.03
Ducula aurorae USNM 344776	38.4	31.0	1.24
Ptilinopus porphyraceus UWBM 42903	20.3	22.1	0.92
Ptilinopus purpuratus DMNH 60555	20.1	25.5	0.79
Ptilinopus rarotongensis UWBM 42521	19.4	24.8	0.78
Ptilinopus dupetithouarsii USNM 318785	20.6	24.1	0.85
Ptilinopus perouseii UWBM 42842	21.4	23.0	0.93
Gallicolumba nui BPBM 171879, 176000	35.1	51.5	0.68
Gallicolumba rubescens USNM 290145, BPBM 162585, 170299, 175095, 175098, 175100, 176001	19.1	30.1 28.7–31.6	0.63
Chalcophaps indica USNM 557062	23.0	28.8	0.80
Caloenas nicobarica USNM 557091	39.3	42.6	0.92

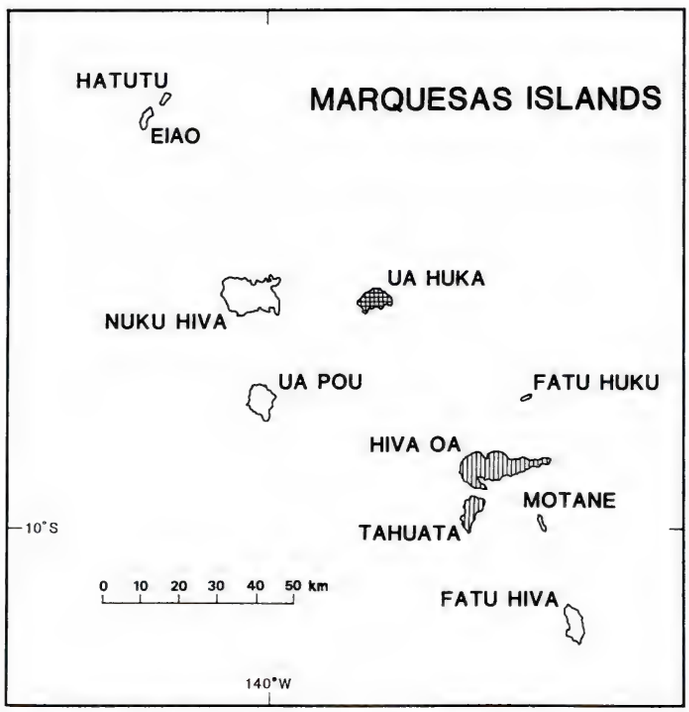

Figure 6. The Marquesas Islands. Vertical lines indicate the islands where bones of *Gallicolumba nui* have been found. Horizontal lines indicate the islands where bones of *Macropygia heana* have been found.

1989). For example, bones of the extirpated pigeon *Ducula aurorae* (Peale 1848) have been found on Atiu and Mangaia (Cook Islands) and on Henderson Island. Bones of the extirpated *Gallicolumba erythroptera* have been found as well on Atiu and Mangaia. The broad prehistoric ranges of *G. nui* and *D. galeata* have already been discussed. Two extinct parrots, *Vini vidivici* Steadman and Zarriello 1987 and *V. sinotoi* Steadman and Zarriello 1987, originally described from the Marquesas Islands, are now known from Huahine (Steadman, 1989). As the ar-

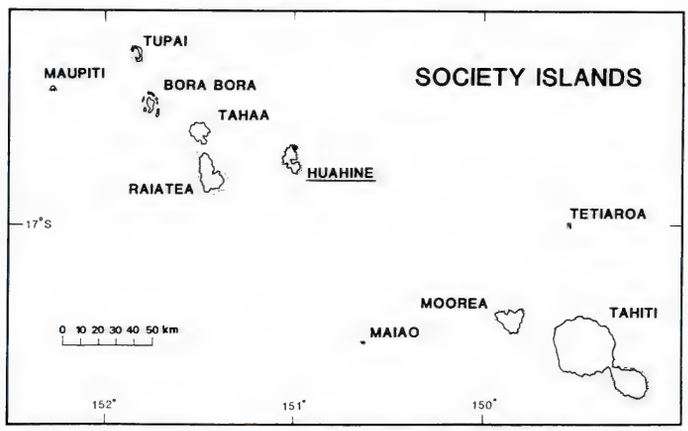

Figure 7. The Society Islands. Bones of *Gallicolumba nui* and *Macropygia arevarevauupa* have been found on Huahine (underlined).

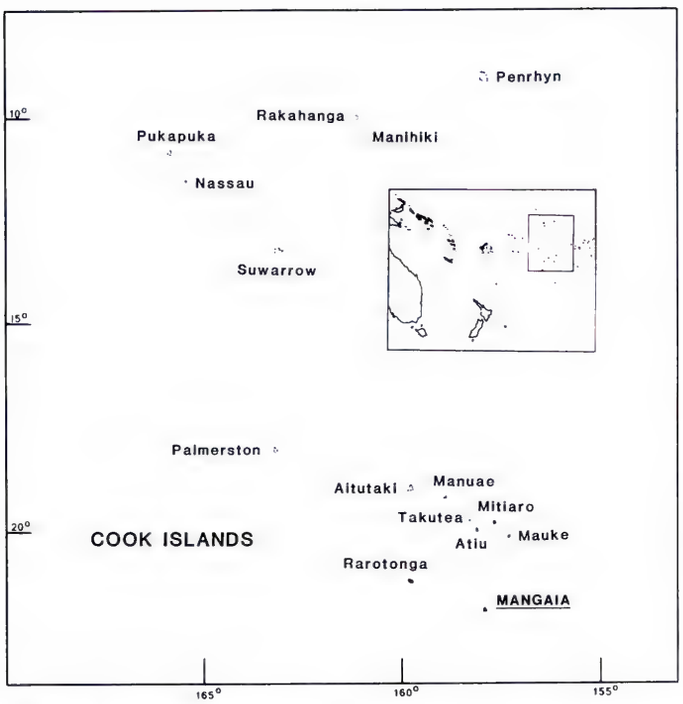

Figure 8. The Cook Islands. Bones of *Gallicolumba nui* have been found on Mangaia (underlined).

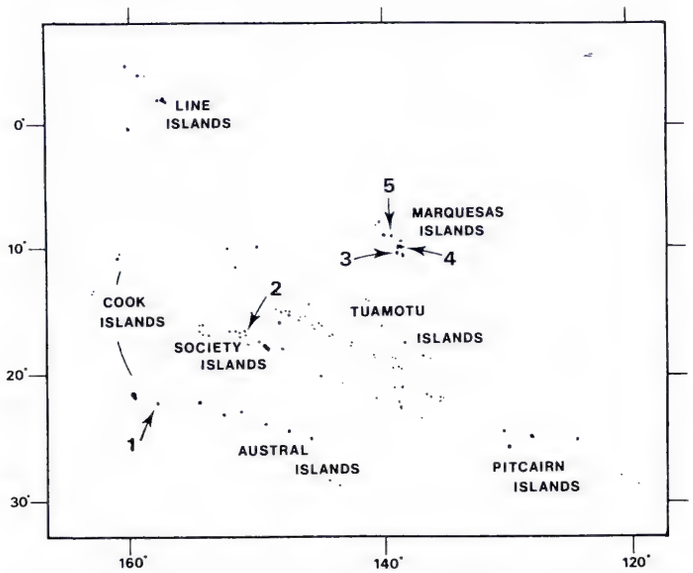

Figure 9. East Polynesia. Arrows indicate the islands, detailed in Figs. 6–8, where bones of *Gallicolumba nui* have been found. Bones of *Macropygia* spp. have been found as well on Ua Huka (*M. heana*) and Huahine (*M. arevarevauupa*). **1,** Mangaia; **2,** Huahine; **3,** Tahuata; **4,** Hiva Oa; **5,** Ua Huka.

cheological record of East Polynesian birds improves, it will be interesting to learn if *M. arevarevauupa* was truly confined to the Society Islands, if *M. heana* was truly confined to the Marquesas, and if other species of *Macropygia* occurred elsewhere in East Polynesia.

The apparent vulnerability of *Macropygia* spp. in East Polynesia suggests that the ranges of living species of *Macropygia* in Melanesia and elsewhere may also have been altered by human activity. In the Bismarck region, for example, the "checkerboard" distribution of *M. mackinlayi* and *M. nigrirostris* as well as the range patterns of the entire assemblage (four species) of cuckoo-doves (see Diamond, 1975:388, 391–400) may be, in part, a result of human influence. Historical evidence, in the form of identified bones from dated prehistoric contexts, is needed to learn how natural these distributions really are.

As outlined in the Introduction, the modern distribution of *Macropygia* does not include Polynesia but reaches its eastern limit in Vanuatu (Fig. 1). Realizing the past occurrence of *Macropygia* in East Polynesia (Fig. 9), it would seem virtually certain that many extinct island populations, and an unknown number of species, of *Macropygia* await discovery among the hundreds of islands between Vanuatu and Huahine and Ua Huka. At the species level, there is very little overlap between the landbird faunas of West Polynesia (Fiji, Tonga, Samoa, and outliers) and East Polynesia. Likewise, there is very little species-level overlap between the landbird faunas of West Polynesia and those of Vanuatu, where *M. mackinlayi* occurs today. The species- and

Table 10. Past and present distribution of pigeons and doves in the Marquesas Islands. Abbreviations: A, archeological record; H, historic (=post-European) record, but no longer survives; NA, no archeological record; X, modern record, certainly or probably survives; *, extinct species.

	Nuku Hiva	Hiva Oa	Ua Pou	Ua Huka	Fatu Hiva	Tahuata
Ducula galeata, "Nuku Hiva" Pigeon	X	A		A		A
Ptilinopus dupetithouarsii, White-capped Fruit-Dove	X	X	X	A, X	X	A, X
Ptilinopus mercierii, Red-moustached Fruit-Dove	X	A, H		A, H?	H?	
Gallicolumba rubescens, Marquesas Ground-Dove	A, H	A		A		A
**Gallicolumba nui,* Giant Ground-Dove		A		A		A
**Macropygia heana,* Large Cuckoo-Dove				A		
Total species today	3	1	1	1	1	1
Total species historic	4	2	1	2?	2?	1
Total species with archeological record	4	5	1 NA	6	2? NA	4
Island area (km²)	337	324	104	78	77	53
Island elevation (m)	1,185	1,190	1,232	855	960	1,000
Distance (km) to nearest island	36	3	33	36	40	3

subspecies-level radiation of *Macropygia* east of Vanuatu has been totally obliterated by humans. What little we know of this radiation is from its presumed eastern limit in the Marquesas and a single intervening island, Huahine.

The Polynesian archeological record reveals a much greater overall diversity of pigeons and doves on a single island or within an island group than modern records would indicate. For example, not a single species of columbid is known in modern times on Mangaia, Cook Islands, where bones reveal the past occurrence of *Gallicolumba nui, G. erythroptera, Ducula galeata, D. aurorae,* and *Ptilinopus rarotongensis* Hartlaub and Finsch 1871. On Huahine, Society Islands, where only *P. purpuratus* is known during the past 200 years, bones from the Fa'ahia Site indicate the presence 1,250–750 years ago of *Gallicolumba nui, G. erythroptera, Ducula galeata, D. aurorae,* and *Macropygia arevarevauupa* as well as *P. purpuratus.*

On the Marquesan island of Ua Huka, only a single species of columbid, *Ptilinopus dupetithouarsii,* has been recorded since European contact. The 1,800 archeological bones of columbids from Ua Huka represent six species [*Gallicolumba nui, G. rubescens, Macropygia heana, Ducula galeata, P. mercierii* (Des Murs and Prévost 1849), and *P. dupetithouarsii* (Table 10)]. It may be significant that Ua Huka, an island of intermediate size and elevation and relatively great isolation by Marquesan standards (Table 10), once supported all six species of columbids ever known to occur in the Marquesas Islands. I believe that each of these six species once occurred on every island in the group except perhaps tiny Fatu Huku.

A major goal of determining the natural distribution of columbids and other Polynesian landbirds is to develop a sound program to reintroduce species on islands that were once part of their natural range (Steadman, 1989; Franklin and Steadman, in press). If strict protection were provided to the birds and the remaining limestone forest, it might be feasible to reinstate *Ptilinopus rarotongensis* on Mangaia through translocations from Atiu, although potential interactions with the introduced myna [*Acridotheres tristis* (Linnaeus 1766)] would have to be monitored. It would be difficult to restore much else of Mangaia's original columbid diversity, or any of Huahine's or Ua Huka's original columbid diversity, because (1) some of species no longer exist anywhere; (2) the other species barely survive elsewhere and, thus, obtaining propagules for translocation would be difficult, if not impossible; (3) the fragmented forests of Huahine and Ua Huka are infiltrated by non-native trees and shrubs; and (4) humans and introduced mammals (rats, cats, dogs, pigs, goats, horses) live on all three islands today. Nevertheless, through carefully planned programs of translocation, certain uninhabited islands of East Polynesia may hold a promise of survival in the otherwise bleak saga of Polynesian pigeons and doves.

Table 10. Continued.

Eiao	Hatutu	Motane	Fatu Huku
		X	
	X		X
0	1	1	1
0	1	1	1
0 NA	1 NA	1 NA	1 NA
52	18	16	1
576	428	520	361
4	4	22	27

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STRUCTURE, FORM, AND FUNCTION

ON THE EVOLUTION OF INTRARAMAL MANDIBULAR JOINTS IN PSEUDODONTORNS (AVES: ODONTOPTERYGIA)

Richard L. Zusi and
Kenneth I. Warheit

ABSTRACT. Many marine birds can widen the lower jaw by flexing the mandibular rami at anterior and posterior intraramal hinges (streptognathism). Apparent synovial joints have been described in the posterior intraramal hinge of Cretaceous toothed birds and Tertiary pseudodontorns (Odontopterygia); we demonstrate synovial joints for the first time in the rami of extant pelecaniforms by histological sections and present a morphocline that could serve as a model for the evolution of joints in pseudodontorns. These joints develop from internal ossifications associated with Meckel's cartilage, not from the splenial and angular bones as in Cretaceous toothed birds. Pseudodontorns differ from extant birds in the lack of a bony symphysis of the mandible.

We envision the pseudodontorns as marine birds that captured prey such as fish and squid near the surface while the birds were in flight or swimming. Bowing of the mandible to an extraordinary degree admitted large prey into the throat; pseudoteeth and a hooked maxilla served to secure live prey in jaws that were weakened for grasping by lack of a bony symphysis.

Key words: Odontopterygia, pseudodontorn, Pelecaniformes, Sulidae, *Hesperornis*, streptognathism, jaw mechanics, synovial joints, functional anatomy, evolution.

INTRODUCTION

The upper and lower jaws of living birds are capable of remarkable diversity of motion relative to the braincase. Both are linked to the braincase by movable quadrates—directly in the case of the lower jaw or mandible, and indirectly through the palate and jugal bars in the case of the upper jaw, or maxilla. The jaws open and close primarily by rotation of the maxilla around the craniofacial hinge and of the mandible at the quadratomandibular articulation. In addition, in certain birds each jaw exhibits internal flexibility—dorsoventral bending of the maxilla (rhynchokinesis) and lateromedial bending of the mandible (streptognathism). In this paper, we focus on streptognathism and in particular on the presence of intraramal synovial joints associated with mandibular bending. Well-developed articulation surfaces in an apparent bending zone or hinge of each ramus have been described in the Ichthyornithiformes, Hesperornithiformes, and Odontopterygia (Gregory, 1951; Howard, 1957; Howard and Warter, 1969; Harrison and Walker, 1976). Although hinges are well defined in some living birds, notably marine birds (Yudin, 1961) and some aerial insect eaters (Bühler, 1970), and in the extinct teratorns (Campbell and Tonni, 1980, 1981), synovial joints associated with intraramal hinges have not been described. Here we describe such joints in certain pelecaniform birds and use them as a model for the evolution of intraramal joints in pseudodontorns (Odontopterygia). Comments on certain functional properties of the mandible and on the possible uses of streptognathism in pseudodontorns are included.

METHODS AND MATERIALS

Intraramal hinges and joints were compared in pseudodontorns [holotypes of *Odontopteryx toliapica* Owen 1873 (BMNH 44096), *Pseudodontornis stirtoni* Howard and Warter 1969 (Canterbury Museum AV20,569), and an undescribed species of pseudodontorn (ChM PV4768)], in *Hesperornis regalis* Marsh 1872 (USNM 4978), and in skeletons of all living species of the family Sulidae and representatives of all other pelecaniform families and subfamilies, loons (Gaviidae), grebes (Podicipedidae), albatrosses (Diomedeidae), penguins (Spheniscidae), herons (Ardeidae), storks (Ciconiidae), New World vultures (Vulturidae), charadriiforms (Laridae, Alcidae), and galliforms (Phasianidae). The structure of the intraramal hinge was examined in cleaned skeletons of various seabirds by cutting the hinge of one ramus with bone shears. Additional details of structure and function were determined from dissection of alcohol-preserved jaws and manipulation of water-soaked skulls. Intraramal hinges of spirit specimens of *Fregata minor* (Gmelin 1789) and *Sula leucogaster* (Boddaert 1783) were sectioned (8 microns) in the frontal plane. The original illustrations were drawn in pencil by Zusi using a dissection microscope and drawing tube, or an art projector.

Anatomical terminology is based on Baumel et al. (1979), and scientific names and higher classification of extant birds follow Morony et al. (1975) except for Vulturidae (=Cathartidae). Abbreviations for museums are as follows: Natural History Museum, London, BMNH; Charleston Museum, ChM; and National Museum of Natural History, USNM.

STREPTOGNATHISM

The avian mandible consists of two rami, fused anteriorly in adults into a symphysis mandibularis, here termed "symphysis" or "mandibular symphysis." Lack of a bony symphysis, as used here, means that the rami are unfused and movably joined at the tip, probably by some form of connective tissue. One or

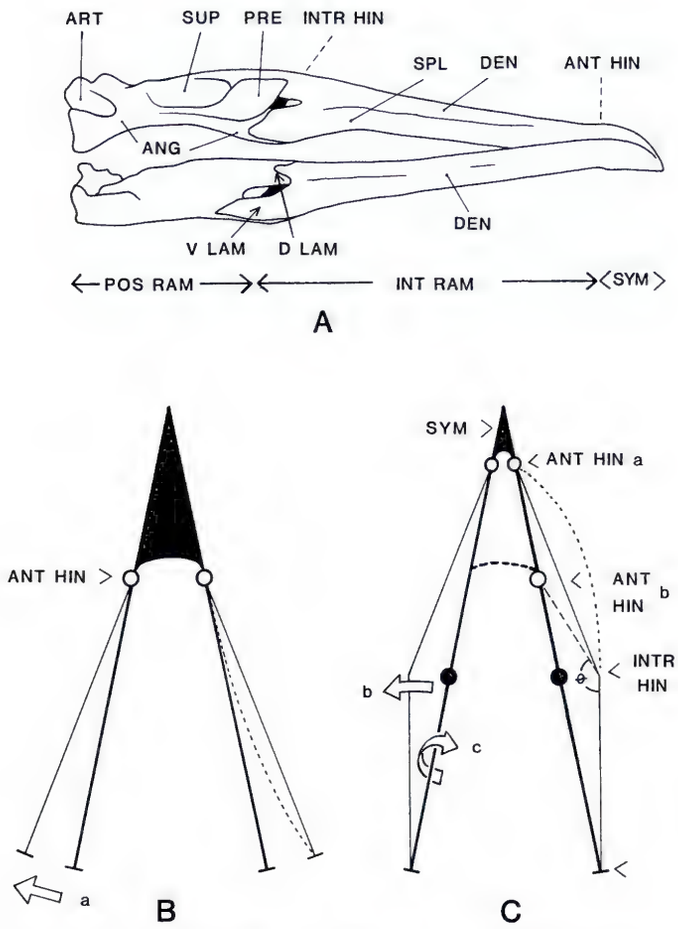

Figure 1. The streptognathous mandible. **A.** *Diomedea nigripes* Audubon 1849, right dorsolateral view; dashed lines indicate positions and orientations of anterior and intraramal hinges. The dorsal and ventral laminae are regions of the intraramal hinge, not individual bones. **B, C.** Diagrams of mandible in dorsal or ventral view; **B** shows lateral spreading of rami (thin straight lines and arrow a) or gradual bending (dotted line); **C** shows lateral bowing of mandible (thin straight lines) with lateral rotation (arrow b) and axial rotation (arrow c) of the posterior ramus. The angle of bending at the intraramal hinge (θ) is more acute (thin dashed line) for a longer mandibular symphysis (heavy dashed line) and anterior hinge b than for a shorter mandibular symphysis (solid black) and anterior hinge a. The dotted line illustrates gradual bending in the absence of an intraramal hinge, as in pelicans. Abbreviations: **ANG,** angular; **ANT HIN,** anterior hinge; **ART,** articular; **DEN,** dentary; **D LAM,** dorsal lamina; **INT RAM,** intermediate ramus; **INTR HIN,** intraramal hinge; **POS RAM,** posterior ramus; **PRE,** prearticular; **SPL,** splenial; **SUP,** supraangular; **SYM,** ramal (mandibular) symphysis; **V LAM,** ventral lamina.

more elastic zones or hinges may be present on each ramus; if two are present, the anterior one is the zona elastica intramandibularis distalis (here termed "anterior hinge"), and the posterior one the zona elastica intramandibularis proximalis (or "intraramal hinge") (Fig. 1A–C). Pars intermedia (the intermediate part) of the ramus lies between the intraramal hinge and the symphysis; pars caudalis (the posterior part) of the ramus is that part posterior to the intraramal hinge.

Mandibular bones are fused extensively, except in the region of the intraramal hinge. The intraramal hinge consists of dorsal and ventral laminae (Fig. 1A), each comprising one or more lateromedially flattened sheets of bone that interconnect the intermediate and posterior parts of the ramus, like hinges on a double-hung door. Apart from the laminae, portions of bones that meet at the intraramal hinge typically form sutures, overlap slightly, or are separated, and they contribute little or no support to the hinge. Intraramal synovial joints discussed later in this paper are found only in the central or ventral portion of the intraramal hinge.

Lateromedial bending within the mandibular ramus may be either abrupt at one or both hinges, or gradual, in the absence of the intraramal hinge. In this paper, bending refers mainly to abrupt bending at the intraramal and anterior hinges. Bending is associated with three kinds of motion (Fig. 1B, C). The first is lateral spreading of the rami (Fig. 1B), which requires lateromedial flexibility of the rami at some point posterior to the symphysis or general flexibility of the ramus. The second is lateral rotation of the posterior part of the ramus about the quadratomandibular articulation (Fig. 1C), which requires flexibility at two points posterior to the symphysis or at one point plus general flexibility of the ramus. The third is axial rotation about the long axis of the posterior part of the ramus (Fig. 1C). These forms of bending may be combined in various ways to produce lateral bowing of the mandibular rami. Bowing capability is highly developed among various water birds, notably penguins, procellariiforms, pelecaniforms, and charadriiforms (see Lebedinsky, 1920; Culemann, 1929; Yudin, 1961; Zusi, 1975). As detailed later, the mechanism of bowing in certain aerial insect eaters (e.g., caprimulgiforms) is somewhat different (Bühler, 1970).

Of the two hinges on each mandibular ramus, the anterior one is simpler, consisting only of a laterally compressed region of flexible bone just posterior to the symphysis. Typically, the orientation of this hinge axis is roughly perpendicular to the long axis of the ramus, in lateral view. By contrast, the intraramal hinge lies near the posterior limit of the dentary (os dentale) and splenial (os spleniale), and its orientation is oblique to the long axis of the ramus—posteroventral to anterodorsal in lateral view (Fig. 1A,2). As already noted, this hinge consists of dorsal and ventral laminae. The dorsal lamina is formed from the anterior end of the supraangular (os supraangulare), embraced on either side by lateral and medial processes of the posterodorsal portion of the dentary. Sometimes it includes the anterodorsal portion of the prearticular (os prearticulare). The broad, flat surfaces of contact between these bones are bound by connective tissue that permits some sliding under shearing stress, but anteriorly the supraangular fuses with the dentary. The ventral lamina comprises the anterior end of the angular (os angulare), embraced laterally by the posteroventral portion of the dentary and medially by the posterior portion of the splenial. The flattened bones are bound by connective tissue and may be unfused or fused at the anterior end of the angular. Bending occurs when the flattened and flexible bone deforms along the hinge axis, and adjacent bones slide against each other in the vicinity of the hinge.

The mandibular ramus is usually laterally compressed at the intraramal hinge and at the anterior hinge, such that the zones of bending are easily recognizable in a dorsal or ventral view of the mandible.

The amount of bending of the ramus (θ) necessary for a given lateral excursion of the intraramal hinge and, therefore, the probability of breakage during mandibular bowing are related to the location of the anterior hinge (Fig. 1C). Perhaps it is for this reason that the anterior hinge is located near the anterior end of the mandible in birds with strong streptognathism. The

symphysis is therefore short in such birds, and it is reduced to the barest bony connection between the rami in pelicans and some penguins.

Yudin (1961), in a survey of mandibular structure in pelecaniforms, stated that pelicans have a well-developed anterior hinge but lack the intraramal hinge. Bones that comprise the intraramal hinge in other pelecaniforms have tight sutures at their contacts in pelicans, and they are extensively co-ossified. The rami are vertically oblong in cross-section and markedly slender anteriorly. Bending is abrupt at the anterior hinge during mandibular spreading. Posterior to the anterior hinge, bending is more gradual and has no relationship to the position of sutures.

All other pelecaniforms have a well-developed intraramal hinge. According to Yudin (1961), in the Phaethontidae the structure of the intraramal hinge is basically like that in gulls and procellariiforms. He claimed that the structure in the Phalacrocoracidae and Fregatidae resembles that in the Phaethontidae, but that the former have a wider and less-defined intraramal hinge. He found the family Sulidae to have an inflated ramus, even in the region of the intraramal hinge. Yudin (1961) did not describe synovial joints associated with the intraramal hinge in pelecaniforms; however, we inferred their presence from bony articulation surfaces in skeletons of the Phalacrocoracidae, Anhingidae, and Sulidae (Fig. 3) and confirmed their presence in *Fregata minor* and *Sula leucogaster* by examination of histological sections (Fig. 4).

RESULTS

INTRARAMAL JOINTS IN EXTANT PELECANIFORMS (FIG. 2)

Yudin (1961) noted the close connection between Meckel's cartilage and both the angular and prearticular bones, and mentioned ossification in the area of Meckel's cartilage that contributed to the anteroventral extremity of the prearticular in charadriiforms, procellariiforms, and some pelecaniforms. In each case, this ossification reached the intraramal hinge without crossing it. We found that ossification in or around Meckel's cartilage is well developed and quite distinct from the prearticular in juvenile skeletons of *Phaethon* Linnaeus 1758, *Fregata* Lacépède 1799, *Phalacrocorax* Brisson 1760, *Papasula* Olson and Warheit 1988, and *Morus* Vieillot 1816 (Fig. 5) and, by implication, in adult specimens of *Anhinga* Brisson 1760 and *Sula* Brisson 1760. We refer to the ossifications in and around Meckel's cartilage in the region of the intraramal hinge as "internal ossifications."

In juvenile specimens of *Phaethon*, the internal ossification consists of a porous, bony tube that replaces Meckel's cartilage. The tube is bounded largely by the prearticular medially and by the supraangular laterally, and it ends at the intraramal hinge (Fig. 5). In the adult, the porous bone is replaced by a smooth-surfaced, hollow, bony projection that is incorporated into the prearticular (Fig. 2). The structure in a juvenile specimen of *Phalacrocorax* was similar to that in a specimen of *Phaethon*, but the structure in adults of the former indicates that at a later stage Meckel's cartilage ossifies anterior to the intraramal hinge as well, as it does in *Papasula abbotti* and other sulids. In adults of *Phalacrocorax*, the ossifications are smooth-walled, hollow tubes supported by internal trabeculae; they meet as a synovial joint at the intraramal hinge (Fig. 2). On either side of the hinge, they are smoothly co-ossified with adjacent bones and their hollow interiors open onto the internal cavities of the intermediate and posterior rami.

In frigatebirds, cormorants (Fig. 3), and anhingas, internal ossifications occupy about one-third the height of the ramus at the intraramal hinge. The bony tube occupies the region of the intraramal hinge between the dorsal and ventral laminae and it forms one or more joints along the hinge axis (Fig. 2). The articulation surfaces are somewhat irregular in outline and tend to develop in the dorsal and ventral rims of the tube. Histological sections of a specimen of *Fregata minor* show that the cartilaginous linings of the joint are thick and irregular and only partially separated by a synovial cavity (Fig. 4A). Nevertheless, a synovial membrane is present, and the structure represents a synovial joint.

In the family Sulidae, a similar bony tube is present, but it is somewhat enlarged and more irregular in shape, and the articulation surfaces are more isolated and variable; an enlarged ventral joint is present (Fig. 3). The vertical extent of the joints is slightly over one-third of the height of the ramus in *Morus bassanus* (Linnaeus 1758) and about one-half of that in *Sula sula* (Linnaeus 1766). Considerable variation in the pattern of joints occurs within *Sula sula*. Enlargement of the joints in *Sula* is at the expense of the ventral lamina; the dorsal lamina is not reduced (Fig. 3). Histological sections through the intraramal hinge of *Sula leucogaster* show that the small, irregular articulation surfaces and the larger ventral surfaces represent well-developed synovial joints, with fully formed synovial cavities, thin cartilaginous linings, and synovial membranes. The large ventral joint is concave anteriorly. Its articulation surfaces are supported by bony trabeculae that parallel the long axis of the ramus in direct line with compression forces (Fig. 4).

Internal ossifications in a juvenile pelican [*Pelecanus erythrorhynchos* Gmelin 1789 (USNM 559663)] were restricted to the immediate vicinity of the quadratomandibular articulation. The rami of adults are essentially hollow, tapering tubes that lack internal ossifications and a differentiated intraramal hinge.

INTRARAMAL JOINTS OF PSEUDODONTORNS (FIG. 6)

A well-preserved but disarticulated intraramal hinge in the mandible of a new species of pseudodontorn (ChM PV4768) clearly indicates the presence of articulation surfaces that occupy about the ventral two-thirds of the intraramal hinge. The dorsal lamina is well developed, but the ventral lamina is absent and replaced by a broad, anteriorly concave articulation. The irregular pattern of articulations dorsal to the large ventral one resembles the pattern in the family Sulidae, except that no trace of a tubular structure is evident. Similar articulations can be seen in the intact, intraramal hinges of *Pseudodontornis stirtoni* and *Odontopteryx toliapica*. By analogy with *Fregata* and *Sula*, we infer that the articulation surfaces in the intraramal hinge of pseudodontorns represent synovial joints. Because such joints in Recent sulids develop from ossifications that originate around or in Meckel's cartilage, we assume a similar origin of the joints in pseudodontorns.

A bony mandibular symphysis was lacking in pseudodontorns. The tip of the mandible was apparently as shown in Fig. 6A; the rami are hollow, are roughly elliptical in cross-section, and bear teeth almost to the tip, suggesting little or no flexibility. The ventral excavation at the anterior end could have been the site of a ligamentous connection between the rami that permitted spreading. The maxilla of the large, undescribed pseudodontorn (ChM PV4768) is deeply concave beneath, terminating abruptly in a hook. When closed, the rami of the mandible apparently lay within the limits of the maxillary concavity. The

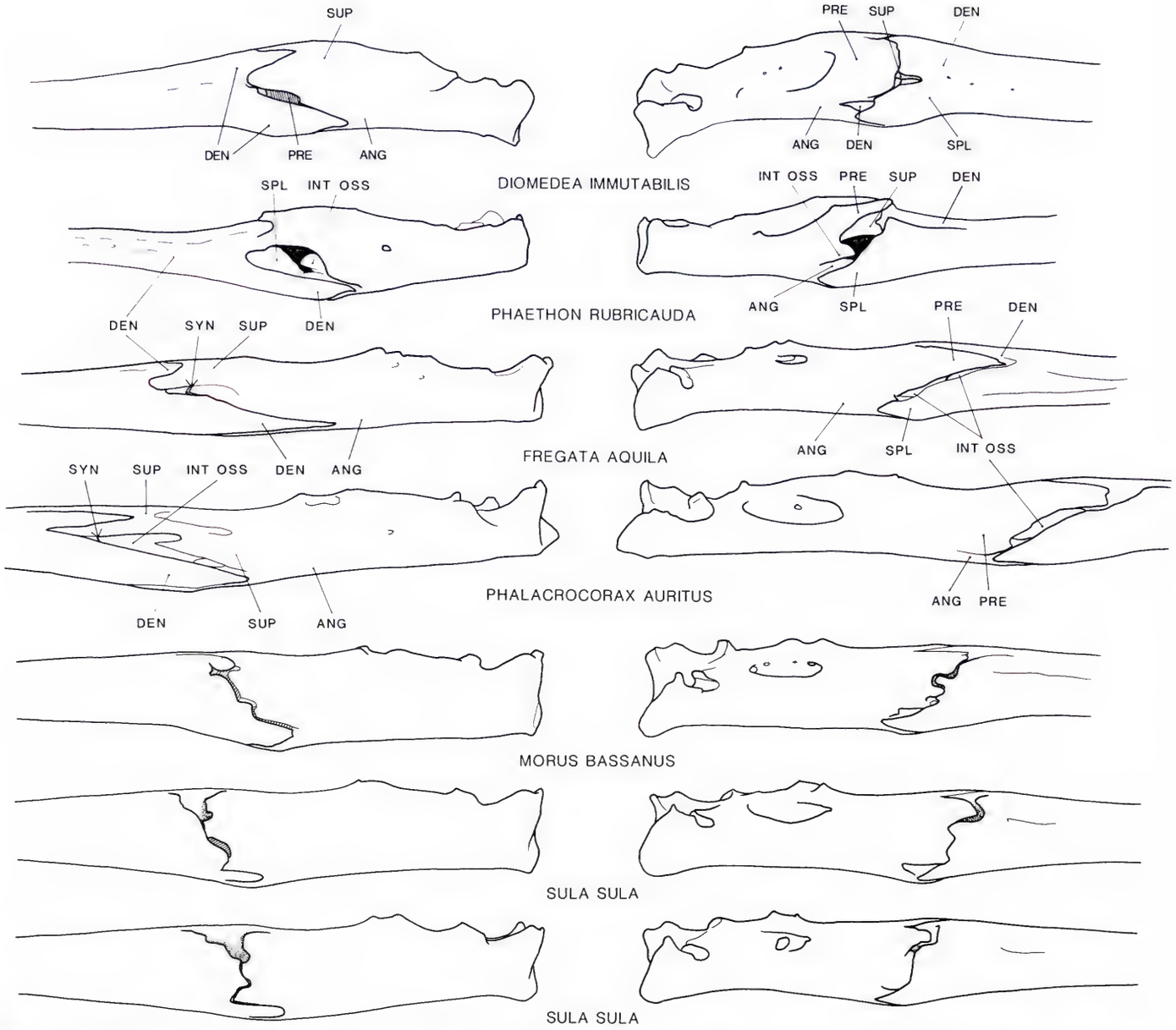

Figure 2. Mandibular intraramal hinges of pelecaniforms and an albatross. Left: lateral view; right: medial view. Abbreviations: **ANG,** angular; **DEN,** dentary; **INT OSS,** internal ossification; **PRE,** prearticular; **SPL,** splenial; **SUP,** supraangular; **SYN,** synovial joint. Sizes adjusted for ease of comparison.

mandibular pseudoteeth were contained within the concavity, and the maxillary pseudoteeth lay lateral to the mandibular rami. Judging from the length of the mandible shown in Fig. 6, and the length of the associated braincase and maxilla, there was little room within the maxillary concavity when the jaws were closed for any rhamphothecal extension of the mandible beyond the bony rami.

DISCUSSION

CONVERGENT EVOLUTION IN PSEUDODONTORNS AND CRETACEOUS TOOTHED BIRDS

In extant pelecaniforms, we find variation among families, genera, and species in the extent of internal ossifications and their associated joints in the intraramal hinge. An inverse correlation exists between the size of the ventral joint and that of the ventral lamina. Extensive development of joints and loss of the ventral lamina puts pseudodontorns at the end of the morphocline: *Fregata* → *Phalacrocorax* → *Morus* → *Sula* → pseudodontorns (Figs. 3, 6). The high development of internal ossifications associated with Meckel's cartilage and synovial joints in the intraramal hinge are not known in other extant birds, and they may, in fact, be a shared, derived character of this group.

Evolution of intraramal synovial joints from internal ossifications is entirely independent from the evolution of intraramal joints in *Hesperornis* (Fig. 7), *Ichthyornis* Marsh 1872, certain non-avian theropod dinosaurs, and mosasaurs, all of which exhibit only a single, ventral joint formed from the splenial and angular (Williston, 1898; Gregory, 1951; Gingerich, 1972).

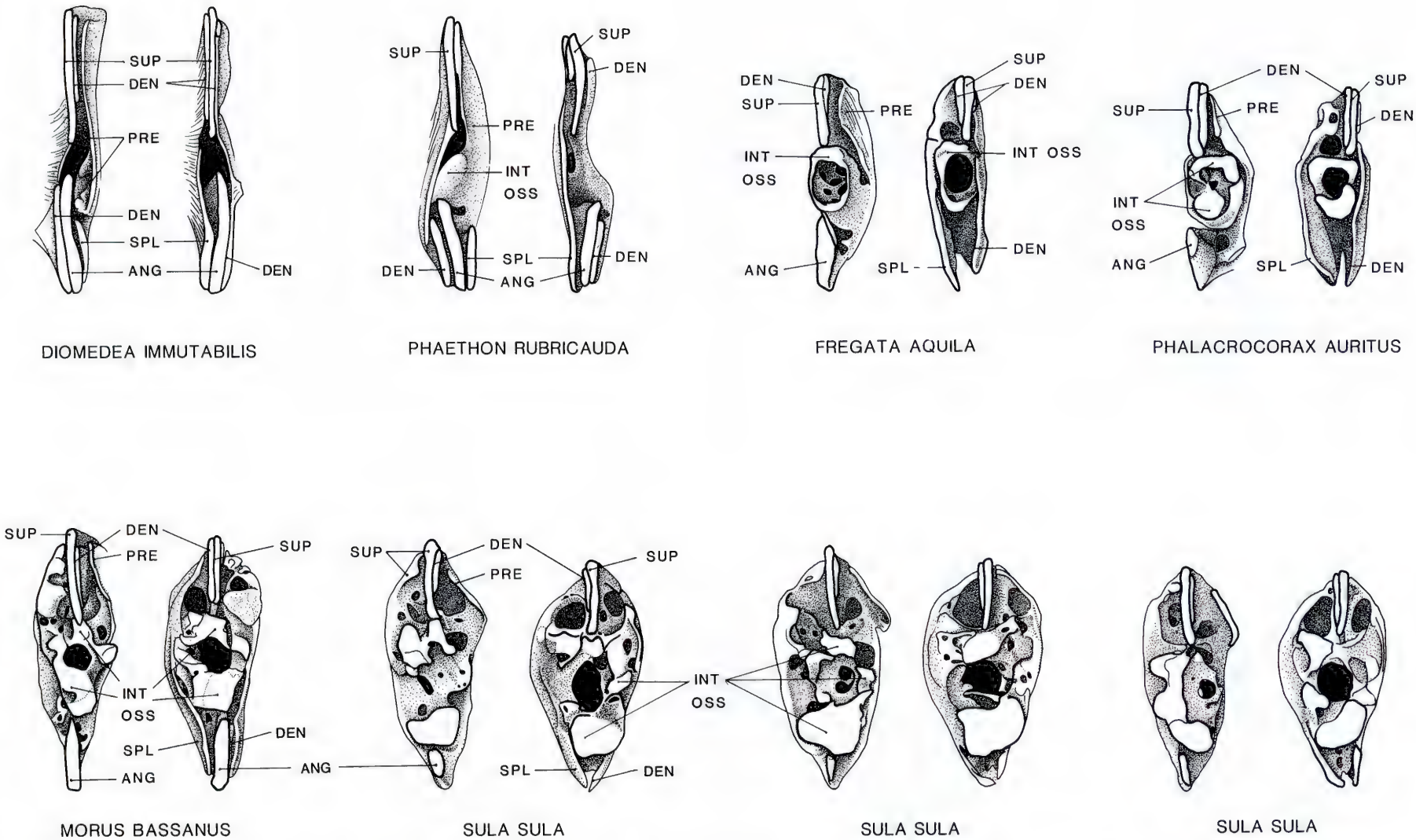

Figure 3. Structure of intraramal joints. Right posterior ramus (left figures) and intermediate ramus (right figures) in end view. Dorsal and ventral laminae (more or less vertical, flattened, unshaded bones) cut in transverse section; articulation surfaces of intraramal hinge in *Fregata*, *Phalacrocorax*, *Morus*, and *Sula* are irregular, unshaded portions of internal ossifications. Abbreviations: **ANG,** angular; **DEN,** dentary; **INT OSS,** internal ossification (not all are labeled); **PRE,** prearticular; **SPL,** splenial; **SUP,** supraangular.

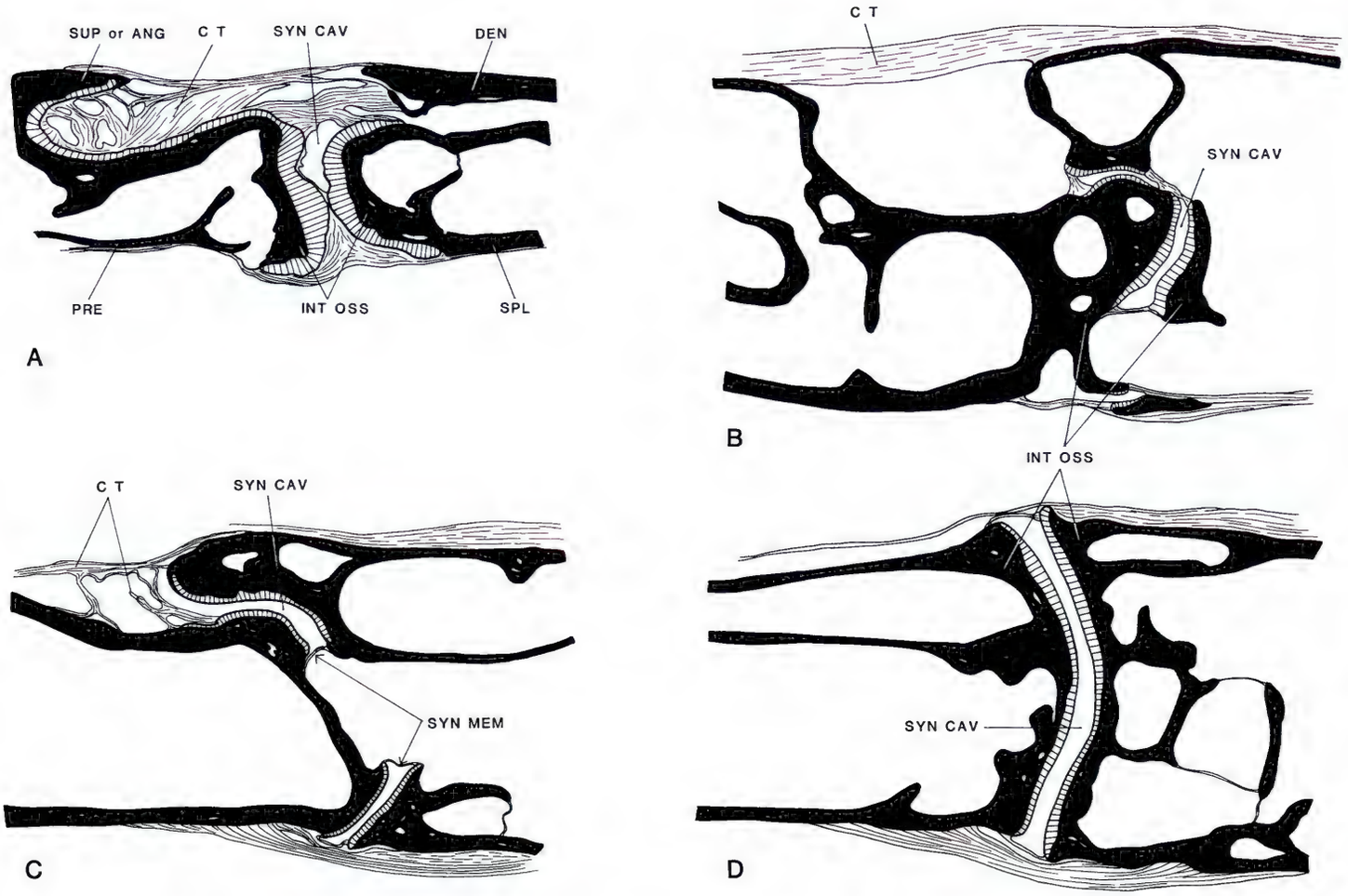

Figure 4. Frontal sections through internal ossifications of left intraramal hinge. Rhamphotheca removed. Anterior toward right. **A.** *Fregata minor.* **B–D.** *Sula leucogaster,* progressively more ventral sections. Bone is solid black; cartilage is hatched. Abbreviations: **ANG,** angular; **C T,** fibrous connective tissue; **DEN,** dentary; **INT OSS,** internal ossification; **PRE,** prearticular; **SPL,** splenial; **SUP,** supraangular; **SYN CAV,** synovial cavity; **SYN MEM,** synovial membrane.

A bony mandibular symphysis was apparently absent also in *Ichthyornis* and *Hesperornis* (Gregory, 1952), and lateral spreading at the tip was undoubtedly enabled by some form of flexible connection between the relatively stout rami. *Hesperornis* resembled pseudodontorns in that the mandibular rami were toothed almost to the tip, probably were not flexible anterior to the intraramal hinge, fitted partially into the maxillary concavity when the jaws were closed, and had little epidermal extension beyond the limits of the bony rami.

FUNCTIONAL ASPECTS OF STREPTOGNATHISM

Lateral Rotation (Fig. 1C)

Lebedinsky (1920), Böker (1939), and Yudin (1961) proposed that lateral bowing of the mandible in many seabirds is initiated by contraction of medial portions of the m. pterygoideus. This muscle simultaneously retracts the palate, thereby depressing the upper jaw and spreading the quadrates, and rotates the posterior part of the mandibular ramus laterally about its quadrate articulation by drawing forward the tip of the medial process of the mandible (processus mandibulae medialis). Such rotation would be slight according to Yudin (1961), who claimed that the occipitomandibular ligament would restrict anterior displacement of the medial process of the mandible relative to the braincase. However, we found, by manipulation of a soaked skull of *Sula sula* with ligaments intact, that the occipitomandibular ligament is slack when both the upper and lower jaws are depressed. There is little doubt that the pterygoideus muscle rotates the quadrates posterolaterally and spreads the rami of the mandible when retracting the palate, but the amount of lateral rotation of the posterior part of the ramus on the quadrate is still unknown.

The question of lateral rotation is particularly interesting in view of a simplified structure of the articulation between the mandible and quadrate in pseudodontorns and pelicans. The medial condyle of the quadrate and its corresponding cotyla of the mandible in these birds are closer to a ball-and-socket than to the tongue-and-groove typical of other pelecaniforms. The posterior condyle of the quadrate, which opposes lateral rotation of the ramus in the opened mandible of most pelecaniforms, is much reduced in pelicans and pseudodontorns. Their lateral condyles and cotylae are broad and shallow and oriented to permit sliding of the opened jaw as it pivots about the medial

condyle of the quadrate during lateral rotation of the ramus (Böker, 1939). Pelicans and pseudodontorns may have an unusual capacity for lateral rotation of the posterior part of the ramus. The structure of the quadratomandibular articulation of most pelecaniforms suggests that lateral rotation of the ramus does not contribute to mandibular bowing.

Lateral bowing of the mandible, with or without spreading of the rami, reduces its length by drawing the symphysis posteriad relative to the posterior part of the ramus (Fig. 8). As explained later, the intermediate part may also be bent ventrad relative to the posterior part.

Axial Rotation and the Oblique Intraramal Hinge

When the quadrates spread laterally, the planes of the quadratomandibular articulations rotate in opposite directions, and the mandibular rami rotate correspondingly about their long axes in opposite directions (Fig. 8A). A vertical intraramal hinge would allow lateral rotation of the rami on the quadrate, but it would also require twisting of the ramus between the quadrate articulation and the symphysis during axial rotation of the posterior ramus. By contrast, an oblique hinge, typical of streptognathous birds, permits both lateral and axial rotation of the posterior part of the ramus without twisting either part of the ramus. The posterior part spreads and rotates while the intermediate part simply spreads and bends slightly ventrad relative to the posterior part (Fig. 8B). Although Howard and Warter (1969) claimed that the intraramal joint of *Pseudodontornis stirtoni* was nearly vertical, we observed it to be oblique in the holotype.

The functional relationships just described assume a vertical anterior hinge that resists axial rotation of the intermediate part of the ramus relative to the symphysis. In pelicans, which lack the intraramal hinge, axial rotation of the posterior part of the ramus is transmitted to the intermediate part during bowing of the rami, but twisting of the ramus is minimized by a slender, anterior hinge that is oblique and flexible in all directions.

Forces within the Intraramal Hinge (Fig. 9)

When a bird grasps and carries prey, the mandible is loaded anterior to the intraramal hinge mainly by the weight of the prey and by resistance of the prey to the force of grasping by the mandible. Posterior to the intraramal hinge, it is loaded mainly by the force of the adductor muscles and forces from the quadrate. These forces produce tension in the dorsal lamina and compression in the ventral lamina (Fig. 9). Flattened and flexible bones are well suited to withstand tension, but they are subject to buckling under strong compression. Synovial joints as found in the intraramal hinge are stabilized under compression by broad surfaces oriented perpendicular to the line of force, but they would be easily disarticulated under tension were it not for the presence of ligaments. Probably for that reason they are restricted to the ventral portion of the intraramal hinge. The advantage of a synovial joint over a flexible lamina may be reduction of the force necessary to bow the mandible while maintaining strong resistance to compression.

Unlike those of most streptognathous birds, the mandibular rami of frigatebirds, cormorants, anhingas, gannets, and boobies are more or less tubular and relatively broad, and this shape is maintained across the intraramal hinge (Fig. 3). Internal ossifications in these birds serve in part to support the lateral walls of the mandibular rami. Synovial joints are a correlate of localized bending of internal ossifications. The large ventral joint of *Sula* may share with the ventral lamina the role of resisting compression, with consequent reduction of the lamina. Lack of the ventral lamina and its replacement by a ventral synovial joint as seen in pseudodontorns is consistent with these functional considerations.

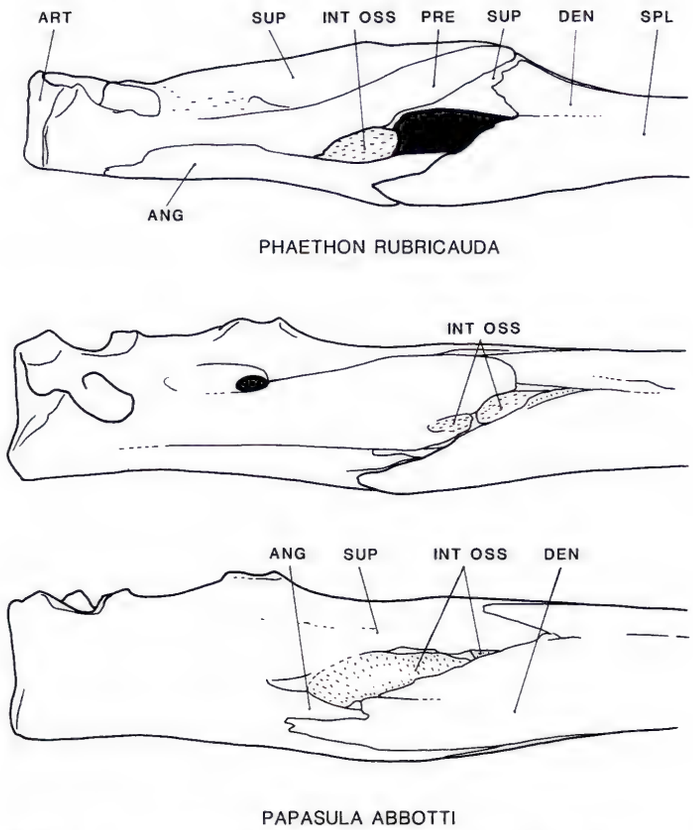

Figure 5. Mandibular intraramal joints of juvenile pelecaniforms. *Phaethon rubricauda* Boddaert 1783 in medial view; *Papasula abbotti* in medial view (above) and lateral view (below); internal ossifications are porous. Abbreviations: **ANG,** angular; **ART,** articular; **DEN,** dentary; **INT OSS,** internal ossification; **PRE,** prearticular; **SPL,** splenial; **SUP,** supraangular. Sizes adjusted for ease of comparison.

Streptognathism in the aerial, insect-eating Caprimulgidae as described by Bühler (1970) contrasts with that of seabirds in many respects: Bowing of the mandible accompanies opening rather than closing of the upper jaw; mandibular bowing is controlled more by muscles acting on the mandible than by spreading of the quadrates; the intraramal hinge includes neither laminae nor synovial joints, but constitutes a syndesmotic schizarthrosis; the intraramal hinge is almost horizontal; the intermediate ramus is elevated against the posterior ramus during depression and bowing of the mandible; and the posterior and intermediate rami rotate in opposite directions during mandibular bowing. The anterior hinge is very weak, and the jaws are used mainly to form a hoop that supports the funnel of the opened mouth rather than to grasp prey.

FEEDING BEHAVIOR OF PSEUDODONTORNS

Hypotheses of behavior inferred from anatomical structure have been falsified frequently by subsequent observation of living

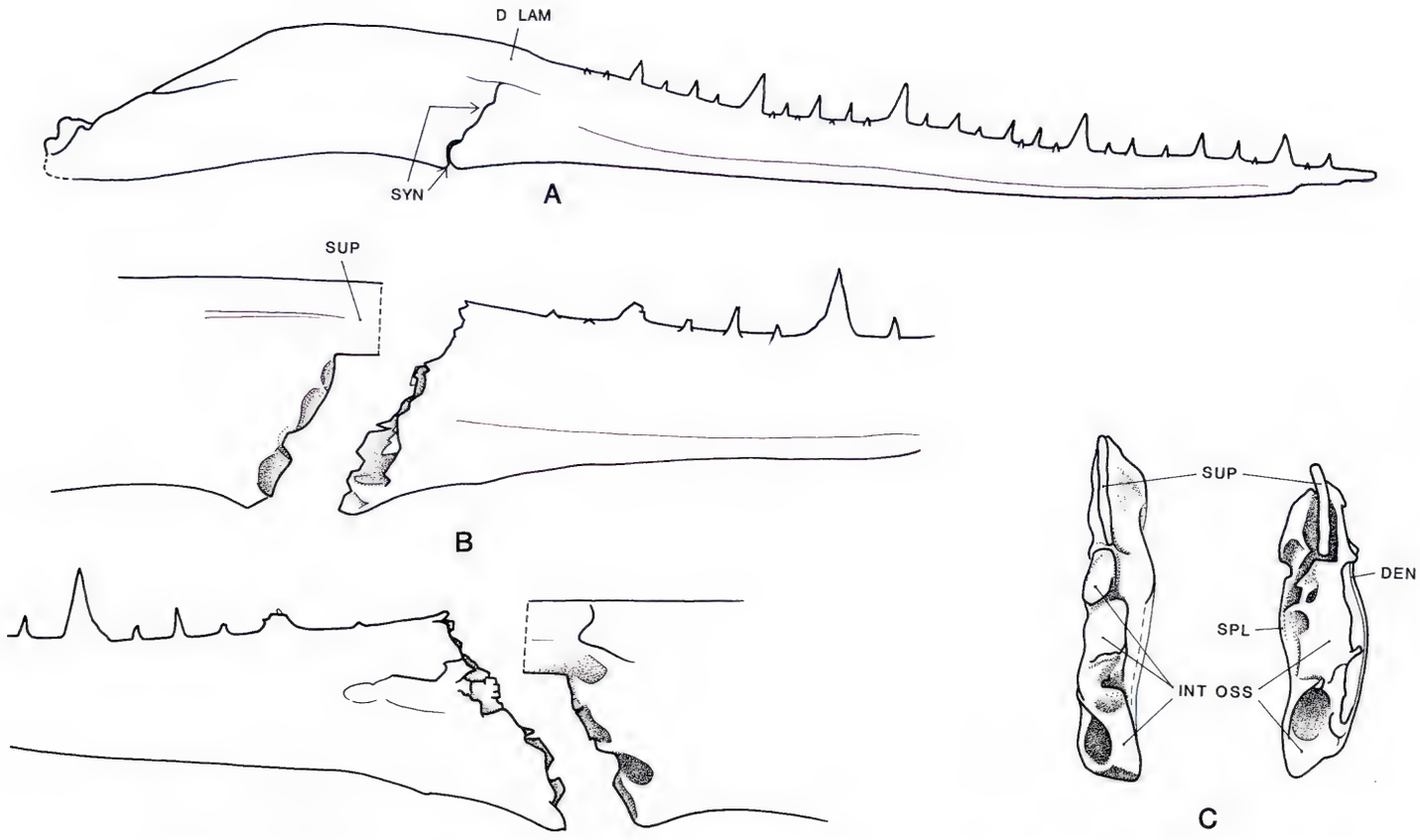

Figure 6. Mandible and intraramal hinge of an undescribed pseudodontorn (ChM PV4768). **A.** Right lateral view of mandible. **B.** Right lateral (above) and medial (below) views of separated intraramal hinge (supraangular broken). **C.** End views of right posterior ramus (left) and intermediate ramus (right). Abbreviations: **DEN,** dentary; **D LAM,** dorsal lamina; **INT OSS,** internal ossification; **SPL,** splenial; **SUP,** supraangular; **SYN,** synovial joint.

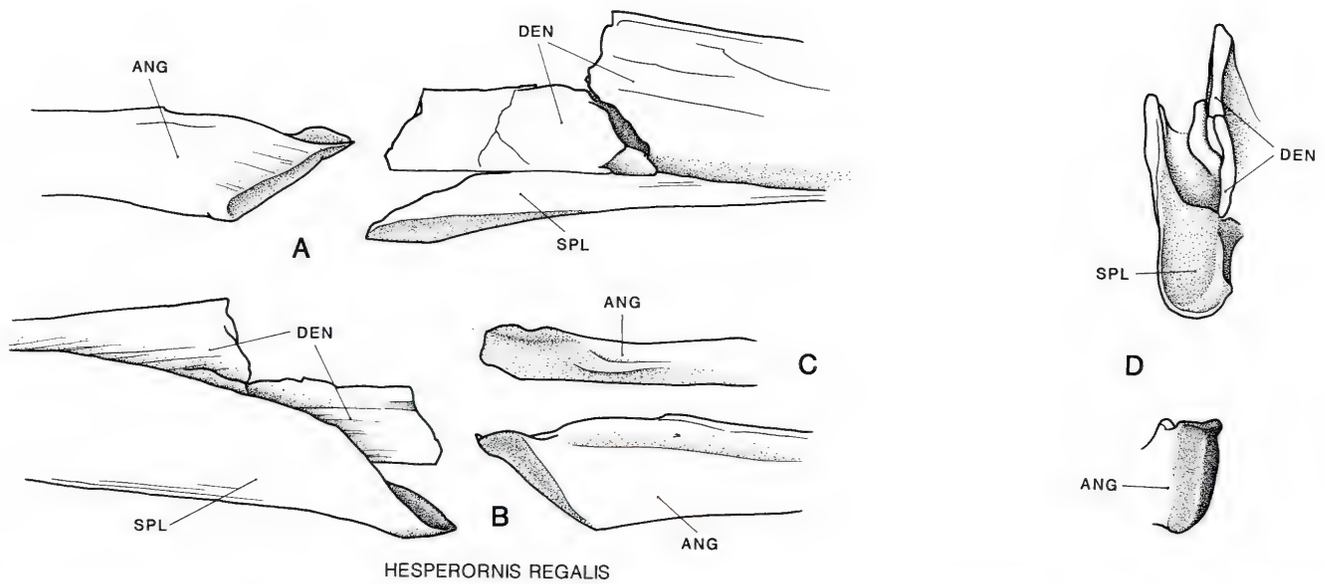

Figure 7. Mandibular intraramal joint of *Hesperornis regalis*. Right ramus separated at joint, dorsal portion of hinge broken or missing. **A.** Lateral view. **B.** Medial view. **C.** Ventral view of angular. **D.** End view of intermediate ramus (above) and angular of posterior ramus (below). Abbreviations: **ANG,** angular; **DEN,** dentary; **SPL,** splenial.

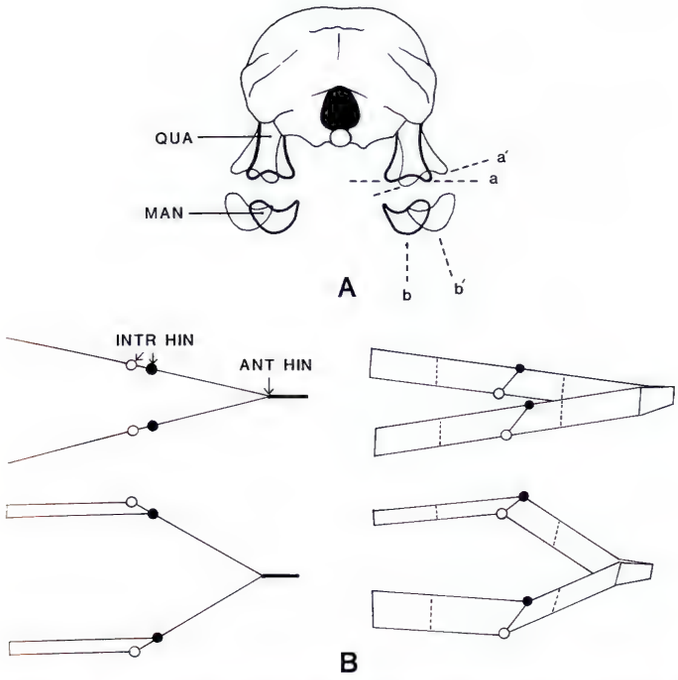

Figure 8. Effect of quadrate motion and oblique intraramal hinge on rotation of rami. **A.** Posterior view of skull and mandible (semidiagrammatic) showing spreading and rotation of quadrates and mandibular rami during retraction of upper jaw (thin lines); plane of quadratomandibular articulation changes (a—a′) and ramus spreads and rotates about long axis (b—b′). **B.** Simplified model of mandible (dorsal view left, dorsolateral view right) in resting (above) and bowed (below) conditions. Because of oblique intraramal hinge (dorsal lamina solid circle, ventral lamina open circle), axial rotation of posterior ramus not transmitted to intermediate ramus. Dotted lines lie perpendicular to long axes of rami. Abbreviations: **ANT HIN,** anterior hinge; **INTR HIN,** intraramal hinge; **MAN,** mandible; **QUA,** quadrate.

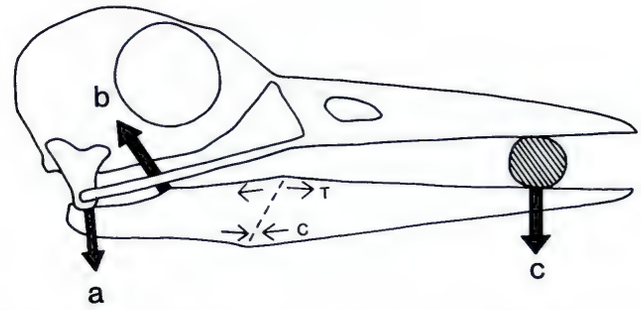

Figure 9. Simplified diagram of forces on mandible. Prey item shaded; large arrows indicate forces from quadrate (**a**), adductor muscles (**b**), and prey (**c**); small arrows indicate tension (**T**) in dorsal lamina and compression (**C**) in ventral lamina.

birds. There is no reason to assume that such hypotheses are more likely to be accurate for fossils, in which they cannot be tested. The following comments on the biological role of streptognathism in pseudodontorns are offered with that caveat.

Pseudodontorns probably did not plunge into the water habitually like a booby, tropicbird, or some terns because their wing structure was highly specialized for gliding rather than flapping flight (Olson, 1985). Pseudodontorns may have grasped prey from the water surface while in flight by a downward nod of the head in the manner of frigatebirds and some terns. It is also possible that they reached into the water for prey while resting on the surface. The tooth-like projections, extending almost to the tips of both jaws, would be well suited for grasping and holding medium-sized to large prey. Prey caught crosswise would probably be tossed and oriented lengthwise before swallowing. The cone-like and spike-like pseudoteeth were well suited for quick release during rapid or repeated toss-and-catch movements used by birds that swallow large prey. The mandible was probably unbowed while grasping and carrying and bowed only for swallowing prey and perhaps for feeding chicks.

As various authors have pointed out, lateral bowing of the mandible in seabirds occurs when the jaws are open and the maxilla depressed. Depression of the maxilla may serve to push prey back into the throat or guard against its escape from the expanded mandible during the process of swallowing. Pseudodontorns have a well-defined craniofacial hinge, implying a highly developed prokinesis. The configuration of their quadratomandibular articulation and unusual flexibility at the intraramal hinge and at the unfused tip of the mandible imply a capacity for strong lateral bowing of the mandible. These specializations would facilitate swallowing of large prey.

Pelicans, certain penguins (*Eudyptes* Vieillot 1816), and mergansers (*Mergus* Linnaeus 1758) are unusual among highly streptognathous water birds in having an extremely slender anterior hinge that bends in all directions, weakening the grasp of the anterior portion of the mandible. Prey capture is facilitated by the pouch in pelicans and by the spiny tongue and mouth lining in penguins. In contrast, mergansers habitually use their jaws, aided by rhamphothecal "teeth," to grasp and carry large fish. We propose that pseudoteeth of pseudodontorns were similarly important for grasping and carrying prey in a mandible weakened by its specializations for streptognathism.

SUMMARY

Streptognathism, or lateral bowing of the mandible, is developed in many marine birds that swallow large prey. Bowing is facilitated by the presence of two internal hinges on each ramus of the mandible, one near the symphysis and one between the intermediate and posterior portions of the ramus (posterior intraramal hinge). The latter hinge consists of dorsal and ventral regions of flat, flexible bone. Pseudodontorns differ from extant birds in having the ventral region of this hinge replaced by a synovial joint, in lacking a fused mandibular symphysis, and by the presence of sharp, tooth-like structures on both jaws. Among extant pelecaniforms, the families Fregatidae, Phalacrocoracidae, and Sulidae possess synovial joints in conjunction with the posterior intraramal hinge, and they suggest a model for the evolution of the synovial joints of pseudodontorns.

Pseudodontorns resemble the toothed Cretaceous birds *Hesperornis* and *Ichthyornis* in having a ventral synovial joint in the intraramal hinge and in the lack of a fused mandibular symphysis, but they evolved these features independently from those Cretaceous birds.

We envision the pseudodontorns as marine birds that grasped prey such as fish and squid near the surface while the birds were in flight or swimming. Soft or slippery prey would have been held easily by the pseudoteeth, and bowing of the mandible to an extraordinary degree admitted large prey into the throat.

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THE MICROSTRUCTURE OF AVIAN AND DINOSAURIAN EGGSHELL: PHYLOGENETIC IMPLICATIONS

Konstantin E. Mikhailov

ABSTRACT. This paper uses eggshell structure as a criterion of sauropsid phylogeny and taxonomy. Eggshell microstructure is used to evaluate relationships within the Archosauria, especially in terms of avian phylogeny, and within the Ratitae. Specific systematic, biostratigraphic, and biogeographic analyses of Eurasian and African ratites demonstrate these principles.

Microstructure characterizes eggshell as a "tissue" and defines the mode of aggregation of mineral and organic elements of micron size. The vertical sequence of zones with different microstructure defines the texture of the eggshell or, as described herein, the principal type of eggshell organization, for any given taxon. Four general types of hard sauropsid eggshells can be discerned: "testudoid" (Chelonia), "crocodiloid" (Crocodilia), "dinosauroid" (Sauropoda, Ornithischia), and "ornithoid" (Aves, Theropoda).

In terms of eggshell microstructure, birds and theropod dinosaurs can be considered as a single branch within the Archosauria. Avian and crocodilian eggshell have no common derived characteristics. Similarities between the eggshell of the Sauropoda and Ornithischia are plesiomorphic.

In respect to macrostructure features, ratite eggshell is most similar to eggshell of theropod dinosaurs and can be considered plesiomorphic within birds rather than derived in ratites. More similarities in eggshell structure are shared between emus and cassowaries than among *Rhea*, *Struthio*, and *Aepyornis*.

Plio-Pleistocene ostrich eggshells from the Palearctic may be divided into three groups that can be interpreted as three forms of *Struthio* (*S. asiaticus, S. transcaucasicus, S. chersonensis*). Eggshell remains indicate that Recent *S. camelus* is a direct descendent of the ostrich lineage of central Asia and they are in accord with the hypothesis of a Eurasian origin of ostriches.

Key words: Aves, dinosaur, eggshell, evolution, microstructure, phylogeny, ratites.

INTRODUCTION

Bone, shell, and other skeletal forms are natural composite materials, a complex of biopolymers and ionic crystals. Mineral components are accumulated in organic "tissues" in the form of polycrystalline aggregates (Crenshaw, 1982). Taxonomically important attributes of polycrystalline skeletal matter are defined by three-dimensional interaction of the organic and mineral phases that are developed on different levels of the matter organization (Lowenstam, 1981; Lowenstam and Weiner, 1983; Barskov, 1988; Golubev, 1988). Eggshell is not excluded from this general principle (Erben, 1970; Simons, 1971; Mikhailov, 1987a, 1987c).

The vertical eggshell units (growth units or exospherites) apparently have a polycrystalline structure that changes during eggshell formation as a result of structural variations of the organic matrix within accumulated calcareous material (Simons, 1971; Krampitz, 1982; Mikhailov, 1987a, 1987c). As a result of these changes, different microstructure zones can be distinguished within the eggshell unit. The presence and vertical sequence of microstructure zones inside the eggshell unit indicate principal microstructure types of eggshell organization, or types of eggshell texture, defined using terminology of mollusk shells. These types are generally stable at and above the taxonomic level of the order.

The relationships within the Archosauria, with respect to avian phylogeny, and within the Ratitae, expressed in the terms of the eggshell microstructure, are the general topic of this paper. The systematic and biogeographical analysis of ostrich eggshells from the Palearctic is discussed in the last section.

METHODS AND MATERIALS

This paper is based on original comparative microscopic studies of avian and dinosaurian eggshells. Fractured and polished surfaces of eggshells, mainly radial sections, were studied by scanning electron microscopy (SEM), with and without chemical treatment, as well as thin sections of eggshell in light microscopes, including polarizing light microscopes (PLM). For methods of chemical treatment, see Erben (1970) and Mikhailov (1987a, 1987c).

In addition to eggshells of modern birds (27 orders, 54 species), crocodiles (2 families, 7 species), turtles (3 families, 11 species), and geckos (2 species), abundant fossil material was studied. Fossil material included dinosaurs, bird and turtle eggshell remains from the Cretaceous of Central Asia (Mongolia, Kazakhstan—82 specimens from 21 localities; China—5 specimens), and, for comparison, dinosaur eggshells from France (Aix-en-Provence—5 specimens) and the United States (Montana, Utah, Colorado—12 specimens). Systematic interpretations of fossil eggshell remains are based on studies of eggs containing embryos and on nests with hatchlings: hypsilophodont and hadrosaurian dinosaurs from Montana (Horner and Makela, 1979;

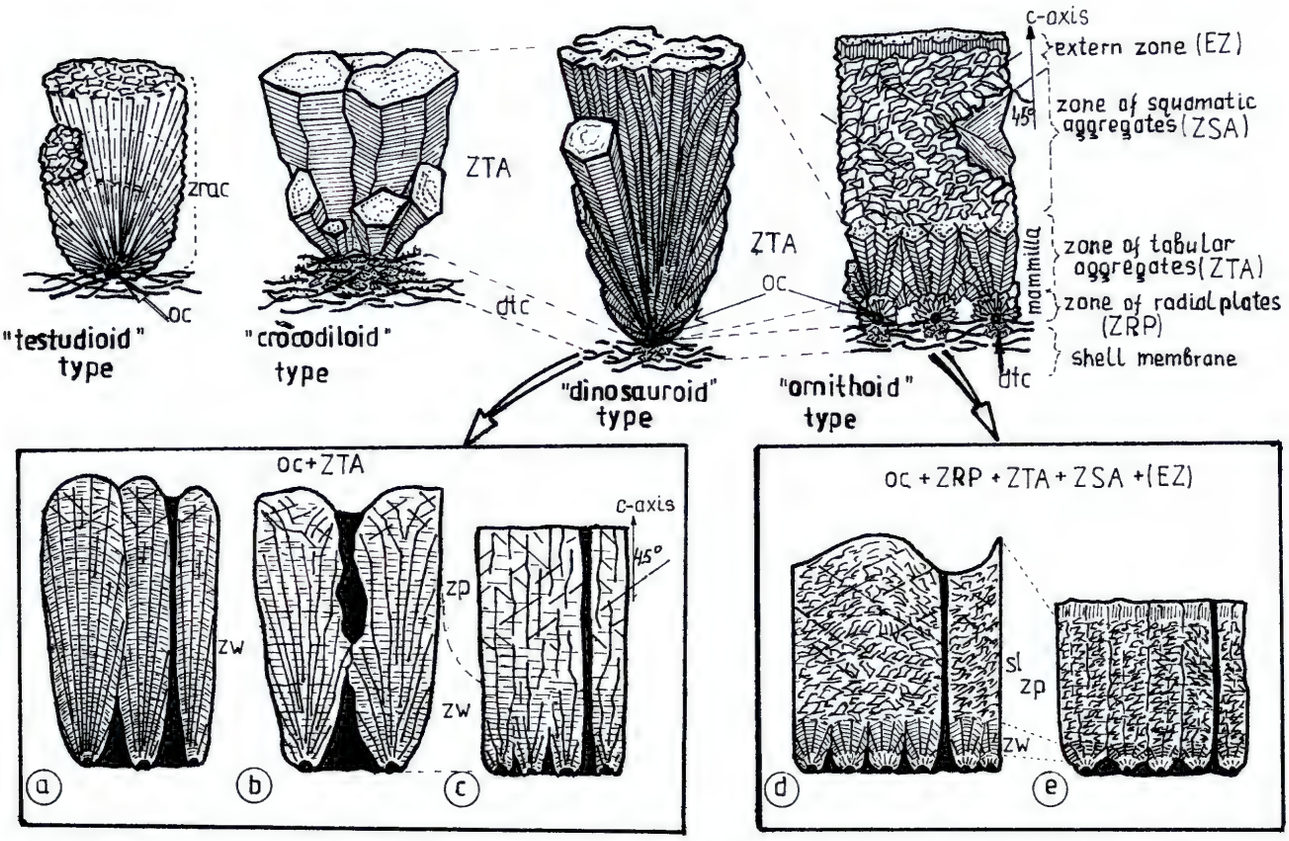


Figure 1. Classification of sauropsid eggshell based on SEM data, shown in radial view of shell units. Four principal types of eggshell organization at microstructure level are shown: "testudoid," "crocodiloid," "dinosauroid," and "ornithoid." Morphological variants occur at macrostructure level; within "dinosauroid," the following morphotypes are seen: (**a**) "discretispherulitic," (**b**) "prolatispherulitic," and (**c**) "spheruprismatic." Within the "ornithoid" group, the following variants occur: (**d**) R = ratite and (**e**) N = neognathous. Abbreviations for microstructure: **DTC,** discrete crystallites; **EZ,** extern zone; **OC,** organic core; **ZRAC,** zone of radiating aragonite crystals; **ZRP,** zone of radial calcite plates; **ZSA,** zone of squamatic aggregates; **ZTA,** zone of tabular aggregates. Abbreviations for macrostructure: **SL,** spongy layer; **ZP,** zone of prisms (prismatic layer); **ZW,** zone of wedges. Dotted line with 45° angle refers to the C-axis of the calcite and shows the crystallographic cleavage plane seen in the "herringbone" pattern.

Horner, 1982); taphonomic data of sauropod dinosaurs from southern France (Aujard and Kerourio, 1986; Breton et al., 1986); protoceratopsians from Mongolia (Andrews, 1932; numerous current, unpubl. data of Mikhailov); and theropod dinosaurs from Mongolia (Kurzanov and Mikhailov, 1989).

Abbreviations are as follows: PIN, Paleontological Institute, Moscow; MHNA, Musée d'Histoire naturelle d'Aix; MOR, Museum of the Rockies, Bozeman; UCM, University of Colorado Museum, Boulder; PLM, polarizing light microscopy; and SEM, scanning electron microscopy. Terminology of eggshell macrostructure and microstructure is after Tyler (1969) and Erben (1970), with some changes and additions (Fig. 1; Table 1). Nomenclature of eggshell types is original.

METHODOLOGICAL REMARKS

Biomineralization proceeds on several levels: (1) nucleation of mineral phase (nucleation centers within protein fibril), (2) primary growth of mineral phase (growth of elementary crystallites along the fibril), (3) secondary growth of mineral phase (aggregation of the elementary crystallites into characteristic blocks and zones), and (4) formation of the skeletal element as a morphological unit (Barskov, 1988; Golubev, 1988).

The biomineralization process is represented on different levels of skeletal organization in different forms (Barskov, 1988). Skeletal elements are specified (1) in macrostructure as a morphological unit and (2) in microstructure and the texture (stratification of the elements) as a tissue. The ultrastructure and the molecular interactions characterize the fundamental relations of the mineral and organic phases.

The structural elements of the different levels of skeletal organization are characterized not only by size but, first of all, by determinants of their own histogenesis (crystallographic, cytobiochemical, physiological control, etc.); thus, they have different taxonomic weight.

In eggshell, we distinguish between (1) superficial features (thickness, microsculpture, pore pattern on the eggshell surface, egg shape and size) and (2) histostructural features of all hard sauropsid eggshells that are constructed the same way. Vertical shell units (0.1–5.0 mm long and up to 0.5–1 mm in diameter) grow from the shell membrane toward the exterior of the eggshell (Fig. 1). Pore canals can be left between them (Tyler, 1969; Erben, 1970).

The description of eggshell structure is based on various features of the vertical shell units at the levels of macrostructure and microstructure.

Table 1. Structure of vertical eggshell growth unit in different groups of sauropsids (from ontogenetically early stages to late ones).

Type and mineral composition	Taxon	Texture: consequence of zones with different microstructure	Macrostructure (morphology of eggshell unit)	Figures
"Testudoid," aragonite	Chelonia	Organic core Zone of radial aragonite crystals (zone with radial aragonite microstructure)	Spherulite with fine radial striation	1–4
"Crocodiloid," calcite	Crocodilia	Aggregates of discrete plates in shell membrane	Basal plate group (rosette)	7
		Zone of tabular crystallite aggregates (zone with tabular microstructure)	Rough unit with rough large wedges	1, 5, 6
"Dinosauroid," calcite	Dinosauria: Sauropoda, Ornithischia	Aggregates of discrete plates in shell membrane Organic core Zone of tabular crystallite aggregates (zone with tabular microstructure)	Basal cap (eisospherite) Elongated unit (subspherulite) with thin wedges or with prisms	1a–c, 8–12
"Ornithoid," calcite	Aves, Theropoda	Aggregates of discrete plates in shell membrane	Basal cap (eisospherite), discrete part of unit	1d–e
		Organic core		
		Zone of radial plates (zone with radial calcite microstructure)	Secondary spherite (base of mammillae)	17–19
		Zone of tabular crystallite aggregates (zone with tabular microstructure)	Zone of wedges (most of mammillae)	16–17
		Zone of squamatic aggregates (zone with squamatic microstructure) Extern zone with vertical crystals	Units in a single layer or as columns with prisms	13–16

Macrostructure—defines an eggshell growth unit as a morphological unit by its characteristics: shape, proportions, size and orientation of the eggshell unit and its large subunits (wedges and prisms). The term "macrostructure zone" is conditional; such zones must be built up during a single physiological phase of the secretory activity of the oviduct epithelium. Features of the macrostructure include the following:

Organic core—a subround organic body at the base of the shell unit.

Eisospherite or *basal cap*—beneath the core, among fibers of outer shell membrane.

Long subunits—of shell unit that radiate from the organic core; known as wedges (ZW) in crocodilians and in some dinosaur eggshells. Wedges form most of the mammillary layer in avian eggshell. In neognathous and some dinosaur eggshell, wedges of mammillary layer phase into vertical prisms (ZP) (column, prismatic, or palisade layer). In ratite and some dinosaur eggshell, vertical units are not well distinguished above the wedges; only a single layer, a spongy layer (SL), can be seen (Fig. 1).

Microstructure—defines an eggshell growth unit as a tissue by its characteristics, its morphological configuration, and arrangement (mode of aggregation) of micron-sized (up to 20–30 mkm) crystalline and organic elements, aggregated in a distinctive way into different zones within eggshell units along its long axis. The vertical sequence of zones with different microstructure defines the texture of the eggshell or, as described herein, the principal type of eggshell organization, for any given taxon.

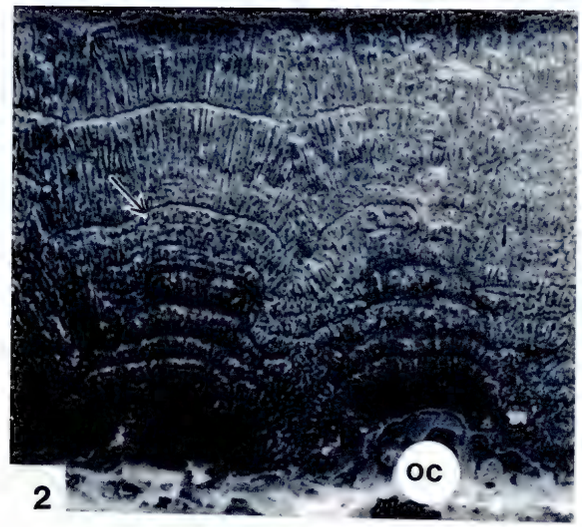
The following elements and microstructure zones can be distinguished (Erben, 1970; Mikhailov, 1987a): organic core (OC); zone of radial aragonite crystals (ZRAC); eisospherite, discrete crystallites among fibers of outer shell membrane (DTC); zone of radial calcite plates (ZRP); zone of tabular crystallite aggregates (ZTA); zone of squamatic crystallite aggregates (ZSA); and external zone with vertical crystals (EZ). The relationship of macrostructure units and microstructure zones is shown in Table 1 and Fig. 1.

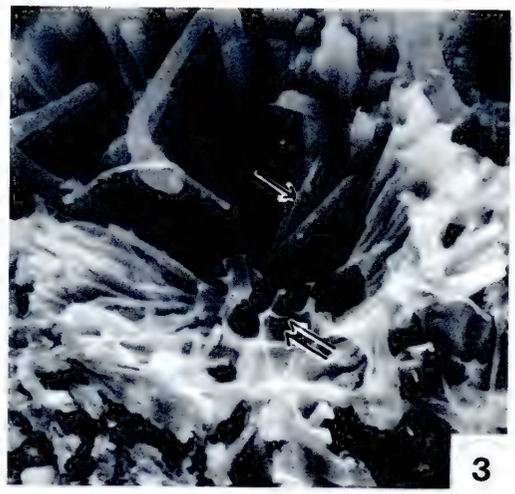
Each microstructure zone is identified by its specific pattern, which is biologically determined and must not be confused with crystallographic patterns of calcite that usually occur in the same zones. Squamatic aggregates are not to be mistaken for the "herringbone pattern" (Erben, 1970), which is of crystallographic origin and represents the fractures along cleavage planes of calcite.

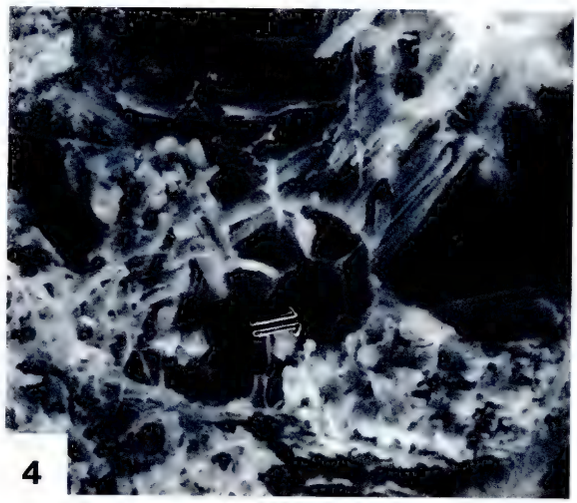
Microstructure features have more taxonomic weight than macrostructure features. Similar types of shell unit macrostructure (morphotypes) can be found within different microstructure types of eggshell organization [avian-like in dinosaurs (dinosauroid) versus neognathous birds (ornithoid), both with large prisms in the upper half of the shell, but of different texture].

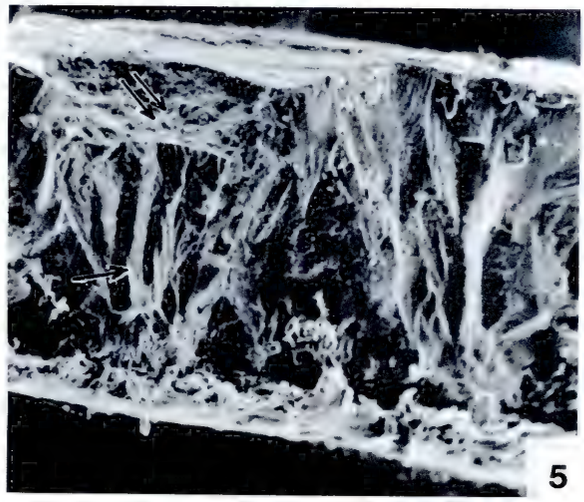
CLASSIFICATION OF SAUROPSID EGGSHELLS

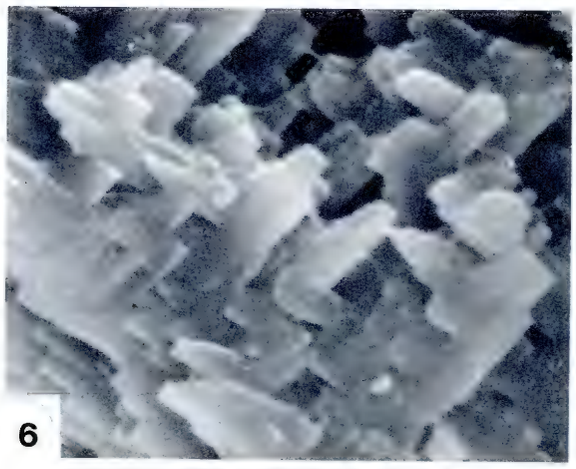
Sauropsids are inclusive of reptiles and birds only, and within this group four general types of hard eggshell organization can be discerned (Fig. 1; Table 1). Eggshells of tuataras and geckos are of unusual types that do not correspond with any of these four; therefore, they will be omitted from further discussion.

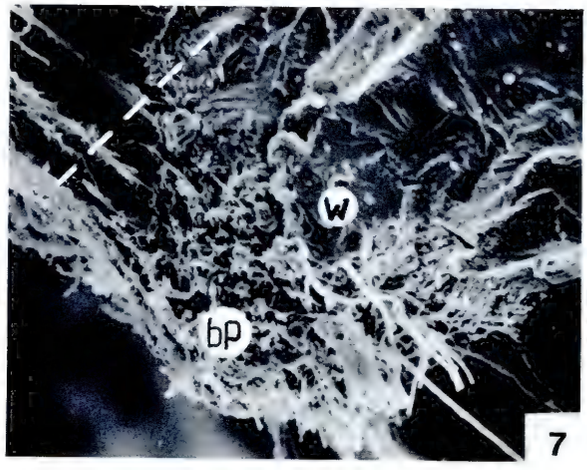












Figures 2–4. SEM photographs of "testudoid" type of eggshell organization; radial view, outside of eggshell is up. **Fig. 2.** Polished radial surface of rigid turtle eggshell (*Dohyma* sp.); chemical treatment 1 percent HCl for 6 seconds. Two eggshell units with organic core (oc). Note accretion lines are very regular (arrow). 330×. **Fig. 3.** Outer view of shell membrane, *Testudo graeca*. 1,000×. **Fig. 4.** View of inner eggshell surface, *Testudo radiata*. Note that shell membrane is removed, although some is left in lower left corner. 500×. Figures 3 and 4 are of fractured base of turtle eggshell units. Note radiating aragonite crystals and broken organic core with "hole loculies" (double arrow) and large organic fibers (arrow).

"TESTUDOID" TYPE (CHELONIA) (FIGS. 2–4)

The eggshell unit consists of a single microstructure zone of aragonite crystals radiating from on organic core in the base (for details, see Erben, 1970; Packard and Hirsch, 1986).

"CROCODILOID" TYPE (CROCODILIA) (FIGS. 5–7)

The eggshell unit consists of a microstructure zone of tabular crystallite aggregates radiating from a group (rosette) of discrete crystallites in the base. An organic core is absent (for details, see Erben, 1970; Hirsch, 1985).

"DINOSAUROID" TYPE (SAUROPODA, ORNITHISCHIA) (FIGS. 8–12)

The eggshell unit consists of a single microstructure zone of tabular crystallite aggregates radiating from an organic core in the base. Two groups of morphotypes, i.e., types of macrostructure, can be distinguished within the "dinosauroid" microstructure type of eggshell organization.

Spherulitic Morphotypes (Figs. 1a, b, 8–11)

Present in Hadrosauria, presumably all Ornithopoda; Sauropoda; tubocanaliculate, prolatocanaliculate, and multicanaliculate eggshells of Erben et al. (1979) and Sochava (1969); for details, see Kurzanov and Mikhailov (1989:fig. 12.2). The eggshell unit of this type consists of a single macrostructure zone, a zone of wedges (ZW) analogous to the mammillary layer (ML) in bird eggshell.

Fossil Material Examined. Eggshells of hadrosaurs from Montana (MOR, uncatalogued; UCM 54475) and Mongolia and China (16 specimens, PIN collections); and sauropod dinosaur eggshells from Aix-en-Provence, France (MHNA), and from Mongolia (PIN, Nos. 2970, 4225).

Spheruprismatic or Prismatic Morphotype (Figs. 1c, 12)

Present in protoceratopsids, presumably all Ceratopsia; hypsilophodonts; angusticanaliculate eggshells of Sochava (1969) and Erben et al. (1979). The eggshell unit of this type consists of two macrostructure zones: a lower zone of wedges (ZW) and an upper zone of prisms (ZP). The last zone is not analogous to the spongy (prismatic) layer in bird eggshell. Both zones have only a tabular microstructure.

Fossil Material Examined. Eggshells of protoceratopsians from Mongolia (8 specimens, PIN collections), eggshells of hypsilophodonts from Montana, and some specimens from Utah (MOR, UCM, uncatalogued).

"ORNITHOID" TYPE (THEROPODA, AVES) (FIGS. 13–19)

The eggshell unit consists of three microstructure zones: secondary spherites with radial plates (ZRP) and organic core (OC) in the base, zone of wedges with tabular microstructure (ZTA) (mammillary layer), zone with squamatic microstructure (ZSA) [spongy layer (SL)]. This type of eggshell was also described earlier as angusticanaliculate eggshell (Sochava, 1969; Erben et al., 1979). Special microstructure zones (extern zone, resistent layer) and two morphotypes (ratite = R and neognathous = N) can be discerned in some bird eggshells (for details, see Erben, 1970; Mikhailov, 1987a, 1987b, 1987c).

Fossil Material Examined. (?)Theropod dinosaur and bird eggshells from Mongolia, Kazakhstan, and China (29 specimens, PIN collections) and one specimen from Montana (UCM 54320).

PHYLOGENETIC IMPLICATIONS

EGGSHELL STRUCTURE AS A CRITERION FOR SAUROPSID PHYLOGENY

From internal eggshell membranes to shell surface, the vertical sequence of the microstructure zones inside the eggshell unit represents a "picture" of eggshell ontogenesis (from earlier to later stages). Each zone reflects a specific physiological stage of the secretory activity of the epithelium. Subdivision of an eggshell unit into microstructure zones is a result of spatial (in different portions of the oviduct) as well as temporal (in one portion) differences in oviduct secretory phenomena. For example, in turtles, where eggshell consists of a single microstructure zone, both the shell membrane and the eggshell are formed in a single long portion of the oviduct, which is homologous to the isthmus in birds (Aitken and Solomon, 1976). In contrast, in birds the process of egg membrane formation is more complicated (Fujii, 1974; Creger et al., 1976). The double membrana testacea (shell membrane) appears in the isthmus. Early stages of mineralization (secondary spherite with radial microstructure) occur only in the terminal part of the isthmus (the red region). Much of the eggshell (mammillary and spongy layers) is formed in the shell gland (uterus). Formation of the mammillary and spongy layers cytobiochemically represent two different processes, where both the organic matrix composition and the speed of mineralization are different (Simkiss, 1968; Georgievskiy and Zablotskaya, 1974; Creger et al., 1976).

Thus, eggshell texture reflects the physiological characteristics of particular groups of parent organisms during eggshell formation and, thus, may be considered useful phylogenetic criteria. Moreover, the types of eggshell organization appear to correlate only with phylogeny. Neither female age and incubation stage nor incubation environments, which vary significantly in birds, have an effect on the arrangements of the microstructure of the eggshell unit. The four microstructure types of eggshell distinguished here are always clear-cut, despite the abundance and

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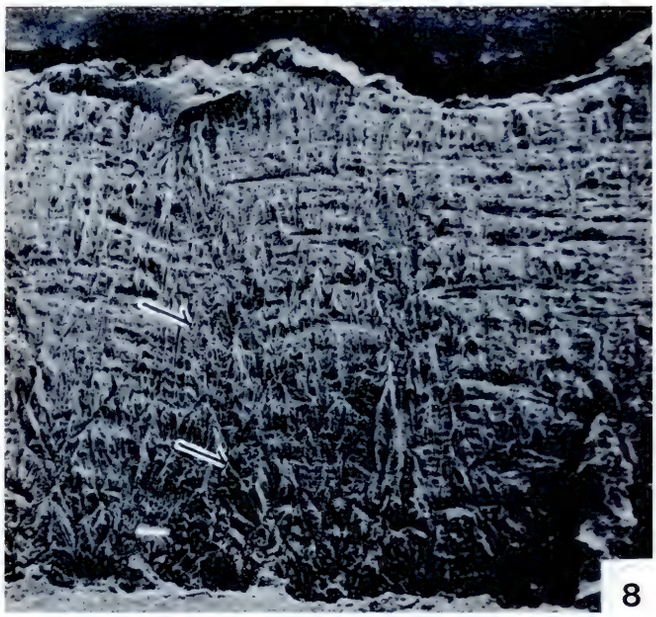
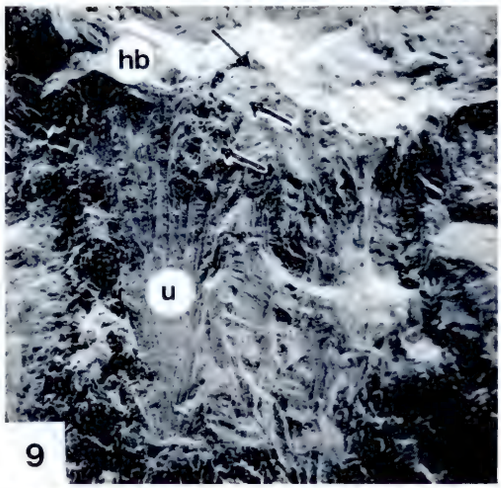
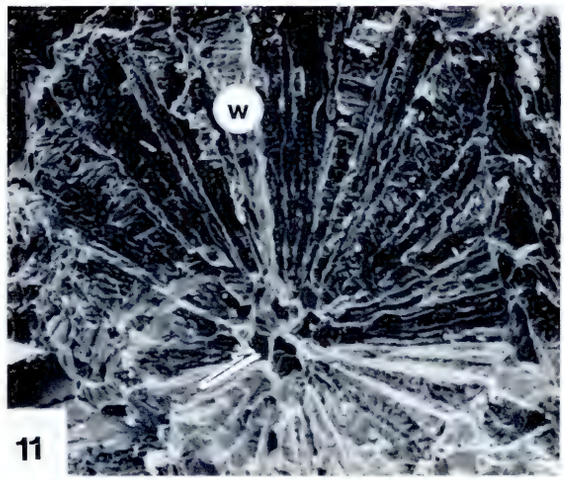
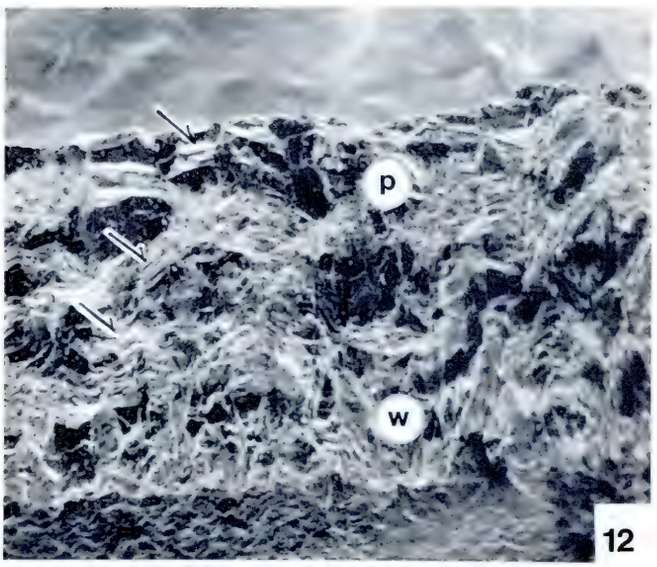
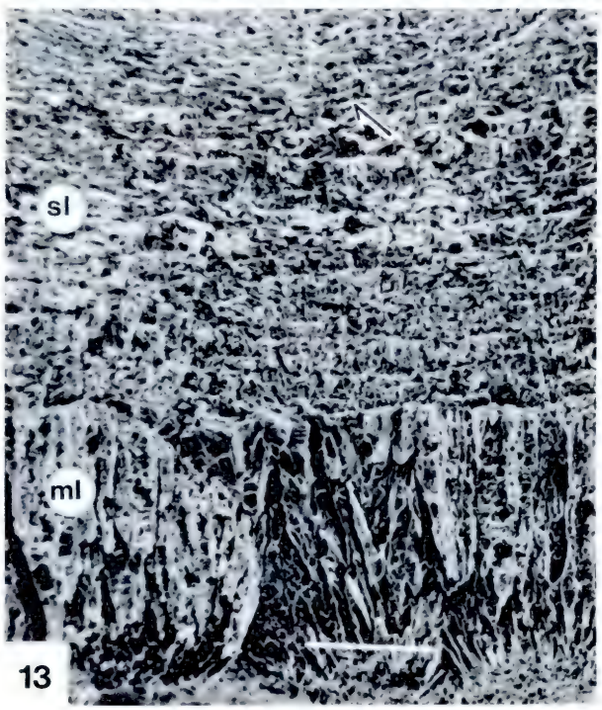
Figures 5–7. SEM photographs of "crocodiloid" type of eggshell organization of *Alligator mississippiensis;* radial view, outside of eggshell is up. **Fig. 5.** Fractured radial surface, two shell units. Note subunits or wedges (arrow) and erosion crater (double arrows) of bacterial origin. 80×. **Fig. 6.** View at basal face of wedge (starting point of growth). Note tabular crystallites. 3,000×. **Fig. 7.** Radial view of fractured base of eggshell unit, dotted line parallel to long axis of unit. Note discrete crystallites of basal plate group (**bp**) among uppermost fibers of shell membrane and transverse fracture of wedge (**w**). 300×.











Figures 8–13. SEM photographs of "dinosauroid" type of eggshell organization; radial view, outside of eggshell is up. **Fig. 8.** Polished radial surface of hadrosaur eggshell; Upper Cretaceous, Montana; UCM 54475; chemical treatment EDTA for 1.5 hours. Note eggshell units with distinct borders (arrows) are the same as the mammillae in "ornithoid" type eggshells (Fig. 13). Fine radial striation pattern as well as acute ends of thin wedges

great diversity of the material investigated. Eggshell in all birds (Class Aves), despite numerous variations in macrostructure, belongs to a single microstructure type, termed ornithoid. Eggshell in all crocodiles (order Crocodilia) also belongs to a single type, termed crocodiloid. The same situation exists with turtles (order Chelonia). Thus, the characteristic microstructure type of eggshell organization appears to be phylogenetically consistent and characteristic at taxonomic levels of order and above.

RELATIONS OF BIRDS AND DINOSAURS AS REVEALED BY THE STUDIES OF EGGSHELL MICROSTRUCTURE

All Archosauria known to have had eggs with hard shells have two common microstructure eggshell zones (Fig. 20, character 3). The zone with discrete crystallites (basal plate group in crocodiles and basal caps in birds and dinosaurs) is ontogenetically the earliest stage of mineralization. Here, discrete plates appear in the upper layers of the shell membranes. In contrast, a zone of wedges with tabular aggregates is well developed and constitutes most of the eggshell thickness in the Sauropoda and Ornithischia. An organic core is present in all known dinosaur and bird eggshell (Fig. 20, character 4). Erben (1970) assumed that in crocodiles the absence of the organic core is secondary. As we know nothing about hard eggshell of the early archosaurs (Thecodontia), this statement must remain open to question. In any event, organic cores have not yet been found in studies of partly mineralized eggshells of lizards and snakes (Lepidosauria; Packard and Hirsch, 1986). In contrast, organic core is well known in turtle eggshells (Figs. 3, 4), which have no crystallized elements common to other sauropsids (Fig. 20, character 1). Presumably, the organic core is an element of the eggshell that originally took part in certain biochemical processes and that later became involved in mineralization. The role of the organic core in mineralization is still open to question.

On the basis of eggshell microstructure, birds and theropod dinosaurs can be considered as a single branch within the Archosauria (Fig. 20, character 5). Derived characters are secondary spherite with radial calcite microstructure and a main zone with squamatic microstructure (spongy layer) that constitutes one-half to two-thirds of the eggshell. As already mentioned, microstructure arrangement of the eggshell unit correlates with the structure of the oviduct. From the comparison of eggshell formation in birds and turtles, together with consideration of the oviduct function in the Sauropoda and Ornithischia (Mikhailov, in prep.), the shell gland is presumed to be an apomorphy in birds and theropod dinosaurs.

A close relationship between birds and theropod dinosaurs has recently been demonstrated once again on traditional osteological materials (Padian, 1982; Thulborn, 1984; Walker, 1985; Kurzanov, 1987). However, data on eggshell microstructure have fundamental significance because most of the mentioned authors based their conclusions on comparisons between the Theropoda and *Archaeopteryx* von Meyer 1861, considering *Archaeopteryx* to be a bird, but not on comparisons of theropod dinosaurs and Recent birds.

It is important to stress that birds and crocodiles have no common derived characteristics in their eggshell microstructure (Fig. 20). Similarity in eggshell microstructure between the Sauropoda, on the one hand, and the Ornithopoda and Ceratopsia, on the other, is plesiomorphic as well.

SIGNIFICANCE OF EGGSHELL STRUCTURE FOR ESTABLISHING RELATIONSHIPS WITHIN THE RATITAE

Eggshells of all Recent and extinct Holocene ratites have many histochemical and macrostructure features in common (Tyler and Simkiss, 1959; Mikhailov, 1987c:table 1). However, most of these such as the strong vertical development of the zone with tabular aggregates (Figs. 16, 17), a relatively small secondary spherite (Fig. 17), the size of the basal cap and organic core, and the tendency of pore canals to branch, do not seem to be phylogenetically consistent, presumably because they appear to be correlated with eggshell thickness. In the only thin ratite eggshell, that of kiwis, and in thin Late Cretaceous eggshells with embryos of paleognathous birds (*Gobipteryx* Elzanowski 1976; Elzanowski, 1981; Kurochkin, 1988), none of these features are well expressed (compare Figs. 16, 17 and Figs. 18, 19). At the same time, in thick eggshells of some neognathous birds, e.g., *Anser* Brisson 1760, *Cygnus* Bechstein 1803, and *Aptenodytes* Miller 1778, the ratite-like features can be seen.

There is, however, one character that is presumably not correlated with eggshell thickness. All ratite eggshell has a spongy layer that is not subdivided (Figs. 1d, 14, 16), whereas in most neognathous eggshell this layer has distinct columns and prisms and is sometimes called the prismatic, or palisade, layer (Fig. 1e). There are some exceptions among the Neognathae, e.g., the Sphenisciformes and Procellariiformes. Moreover, in respect to this macrostructure feature, ratite eggshell is most similar to eggshell of the theropod dinosaurs (compare Figs. 14 and 15) and can be considered plesiomorphic within birds rather than derived in ratites. Thus, monophyletic origin of ratites cannot be demonstrated based on eggshell structure.

However, if we were nonetheless to accept ratite monophyly on the basis of numerous morphological, biochemical, and physiological characters (Houde and Haubold, 1987; Kurochkin, 1988), we could then consider typological relationships within this group in terms of eggshell structure (Fig. 21). Moa eggshell

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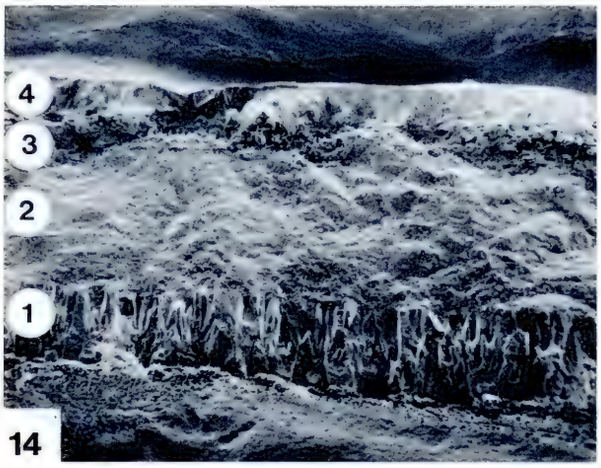
resulted from EDTA etching along C-axis of calcit. 40×. **Fig. 9.** Fractured radial surface of ornithopod (?hadrosaur) eggshell; Upper Cretaceous, Gobi, south Mongolian People's Republic (MPR); PIN no. 3142-454. Eggshell unit (**u**) consists of thin wedges. "Herringbone" pattern (**hb**) in upper part of shell unit is a result of declining of wedges (arrows) and fracturing of calcite along its cleavage planes. 25×. **Figs. 10, 11.** Fractured radial surface of sauropod eggshell; Upper Cretaceous, Aix-en-Provence, France. In Fig. 10, note tabular microstructure of radial subunits (wedges) in upper part of shell unit. There is no squamatic microstructure in the eggshell. 350×. Figure 11 shows an undeveloped shell unit in upper part of double-layered (pathological) eggshell. Wedges (**w**) with tabular microstructure begin to grow from the very center of spherulite. Note transverse sections of wedges (arrow). There are no features of radial microstructure (compare Fig. 17). 225×. **Fig. 12.** Oblique view of fractured radial surface of hypsilophodont eggshell; Upper Cretaceous, Montana; UCM, uncatalogued. Wedges (**w**) in lower half of shell unit are phased to prisms (**p**) in the upper part with no change in microstructure. Oblique light striations and "herringbone" pattern (arrows) are a result of the calcite fracturing along its cleavage planes. 50×. **Fig. 13.** See Fig. 15, "ornithoid" type of dinosaur eggshell, for comparison. Note squamatic microstructure (arrow) in spongy layer (**sl**). 150×.



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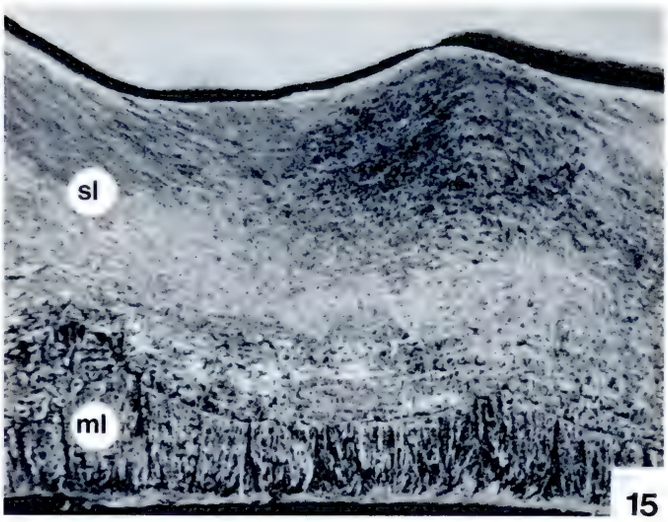

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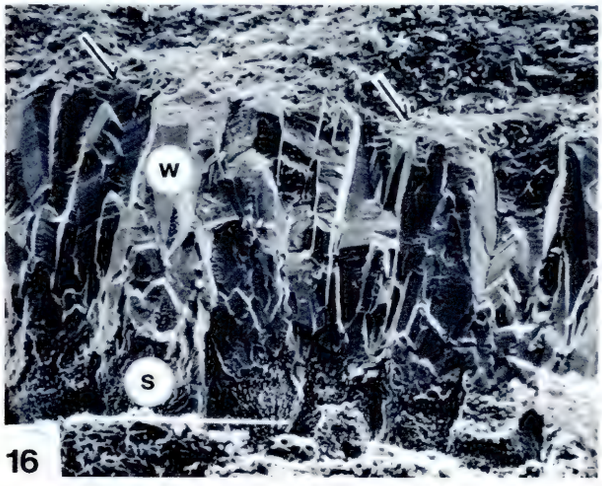

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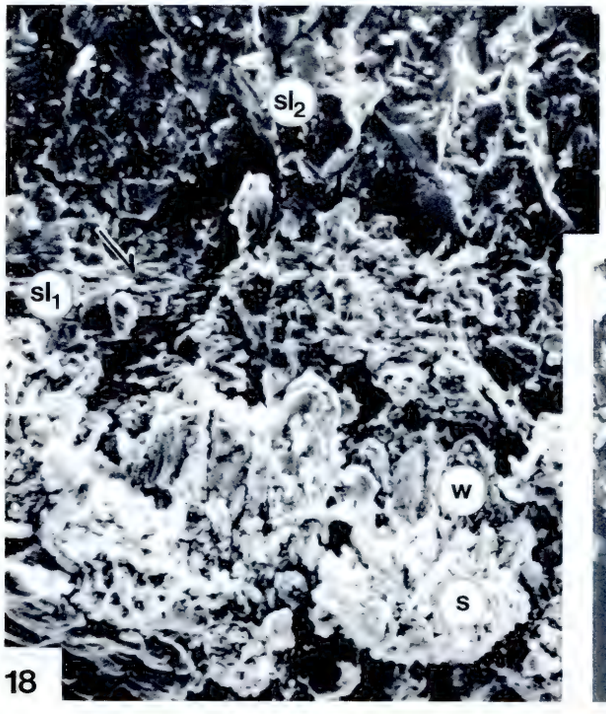

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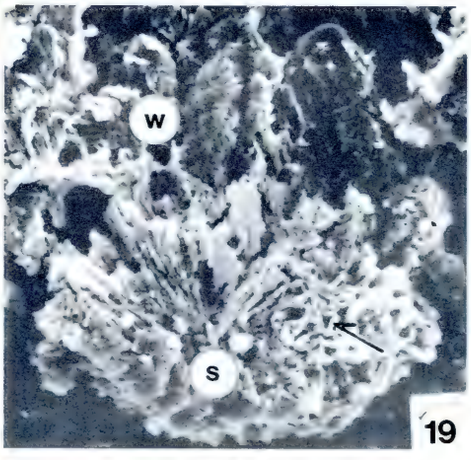

19

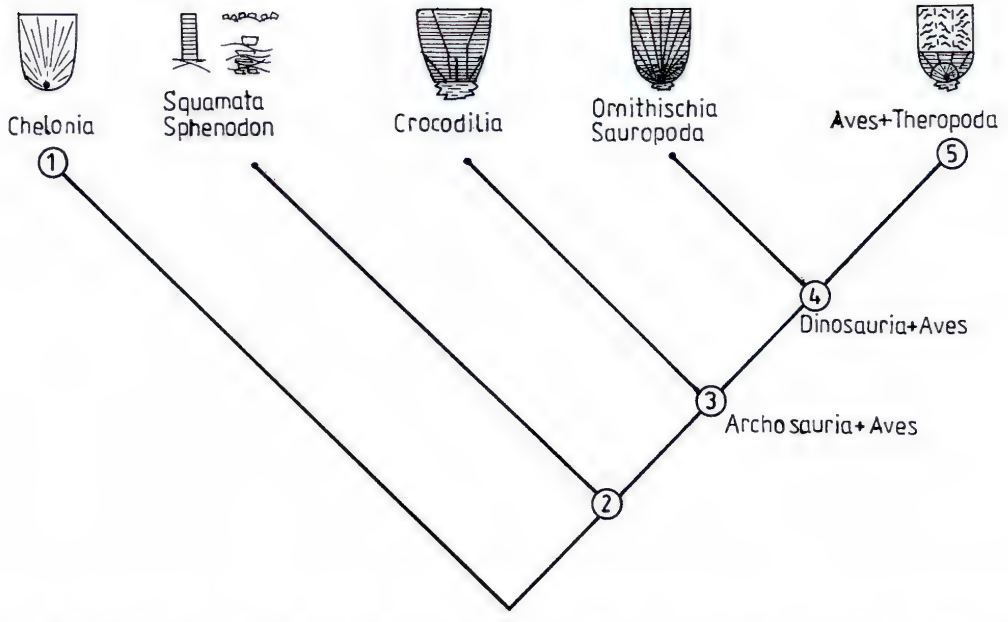

Figure 20. Cladogram of some sauropsid taxa of unequal rank, and with hard eggshell, based on microstructure of eggshell growth units. Derived characters: (**1**) aragonite eggshell; (**2**) calcite eggshell; (**3**) discrete crystallites in shell membrane (**DTC**), zone of wedges with tabular microstructure (**ZTA**); (**4**) organic core (**OC**); (**5**) zone of radial plates (**ZRP**) [in form of secondary spherite (**SS**)], and zone of squamatic aggregates (**ZSA**) (spongy layer).

appears to be the most simple among the Ratitae based on the one eggshell of ?*Anomalopteryx* Reichenbach 1852 studied; the extern zone is absent. Eggshells of all other ratites studied have an extern zone, which is ontogenetically the most recent development. In *Struthio* Linnaeus 1758, *Rhea* Brisson 1760, and *Aepyornis* Geoffroy Saint-Hilaire 1851 eggshell, the extern zone overlies the spongy layer, and pore canals penetrate through it and open onto the shell surface. In *Rhea* and *Struthio* eggshell, the extern zone is thin and one-layered, and these birds also have similar insoluble/soluble nitrogen fractions that are distinct from other ratites (Tyler and Simkiss, 1959). In *Aepyornis* eggshell, the extern layer is thicker and multilayered. Differences in pore patterns of ostrich and elephant-bird eggshell ("struthioid" and "aepyornithoid" types) are of minor taxonomic significance. "Aepyornithoid" pore features repeatedly appear in Neogene ostrich eggshell (Mikhailov, 1986; Mikhailov and Kurochkin, 1988).

Emu and cassowaries (Casuariiformes) clearly possess shared derived eggshell characters. Between the spongy layer and the extern zone lies a very specific resistant layer, rich in organic material (Tyler and Simkiss, 1959; Board and Tullett, 1975; Penner, 1984; Fig. 14). The extern is transformed morphologically into a granular layer with large discrete granules, and the pore canals terminate on the border between the spongy and resistant layer. The organic subround bodies of the resistant layer are nothing other than organic cores that normally lie within avian eggshell on the surface of the shell membrane before the eggshell forms. It does not occur in the shell gland but, rather, in the terminal part (red region) of the isthmus (Richardson, 1935; Wyburn et al., 1973). To explain this phenomenon, it is advantageous to assume that after secretion of the spongy layer the egg returns from the shell gland to the red region and then again moves to the shell gland, where granular layers must appear and the mineralization will be completed (Mikhailov, 1987b).

The data of amino acid composition of proteins of the shell membrane and soluble eggshell component (Krampitz et al., 1974) represent a very special aspect of shell and membrane

←

Figures 14–19. SEM photographs of "ornithoid" type of eggshell organization; in radial view, outside of eggshell is up. **Fig. 14.** View of four horizontal layers of fractured radial surface of eggshell of *Dromaius novae-hollandiae:* (**1**) mammillary layer overlying shell membrane, (**2**) spongy layer, (**3**) resistant layer, and (**4**) granular layer. Note absence of vertical units (columns, prisms) in spongy layer. 50×. **Fig. 15.** Polished radial surface of ?theropod dinosaur eggshell, Upper Cretaceous, east Kazakhstan (Tajzhuzgen River); PIN No. 2970/8; chemical treatment EDTA for 1.5 hours. Note distinct border between mammillary layer (**ml**) and spongy layer (**sl**) and absence of vertical units (columns, prisms) in spongy layer. 35×. **Fig. 16.** As in Fig. 14, mammillary layer with secondary spherite (**s**) and wedges (**w**). Note distinct border between mammillary and spongy layers (arrows) and squamatic microstructure in spongy layer. 200×. **Fig. 17.** As in Fig. 16, note distinct irregular border (single arrows) between the radial microstructure of the secondary spherite (**s**) and the tabular microstructure (double arrow) of the wedges (**w**). 1,000×. **Figs. 18, 19.** Fractured radial surface; shells from eggs with embryos of paleognathous birds (*Gobipteryx*); Upper Cretaceous, Gobi, south MPR, PIN coll. number 3142. In Fig. 18, note fine radial microstructure in secondary spherite (**s**), wedges (**w**), unaltered inner part of spongy layer (sl_1) with squamatic subunits (arrow) and recrystallized upper part of spongy layer with large prisms of diagenetic origin (sl_2). 850×. In Fig. 19, as Fig. 18, note elements of organic matrix (sheaths of crystalline elements) in secondary spherite (arrow). 1,500×.

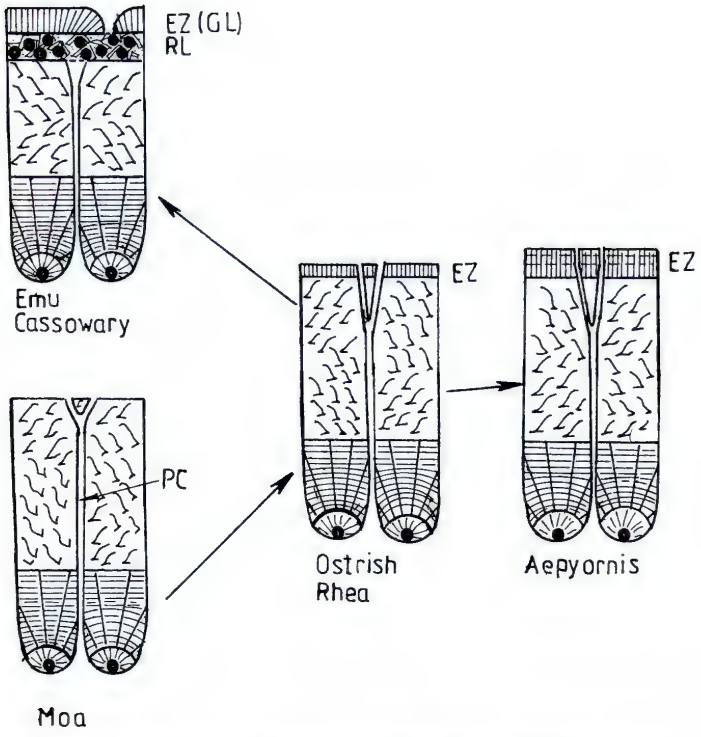

Figure 21. Grades of evolution in upper part of eggshell in some Recent and fossil (Holocene) ratites. Radial view of shell units; not to scale. The branching patterns do not necessarily represent the correct phylogenetic relationship of taxa (see text). **EZ,** extern zone; **GL,** granular layer; **PC,** pore canal; **RL,** resistant layer.

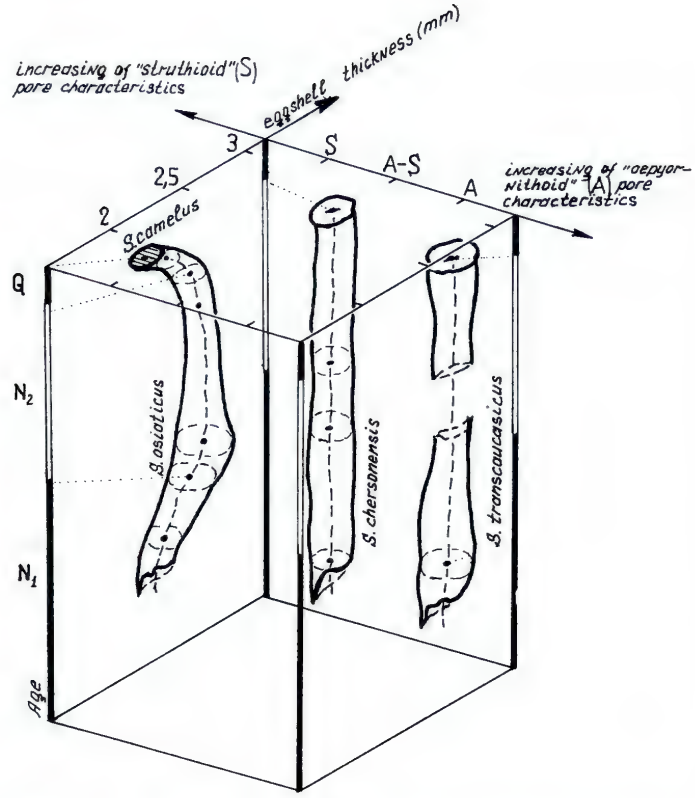

Figure 22. Diagram of eggshell featuring chronological changes in three evolutionary lines of Neogene *Struthio*. X-axis, tendencies in changing pore patterns, from "struthioid" to "aepyornithoid"; Y-axis, eggshell thickness in mm; Z-axis, age scale (see text).

material organization. Nevertheless, it is noteworthy that in the main they are in accordance with microstructure data of eggshell structure. The most similarity was revealed within the order Casuariiformes, and some relationship between *Rhea* and *Struthio* was noted. Surprisingly, the composition of the membrane and shell of *Apteryx australis* Shaw 1813 is different from that of the other taxa of the Ratitae (Krampitz et al., 1974).

HISTORY OF RATITE EGGSHELL FROM THE PALEARCTIC AND THE NEOGENE OSTRICH

Geographical and stratigraphical analysis of eggshell pore pattern diversity shows that all ratite eggshell remains from the Neogene and Pleistocene of the Palearctic and Africa are referrable to the order Struthioniformes, family Struthionidae, and many of them to the genus *Struthio* (Mikhailov and Kurochkin, 1988; Mikhailov, 1988). Plio-Pleistocene ostrich eggshells from the Palearctic may be divided into three groups that can be interpreted as distinct, but similar, forms of *Struthio*. These eggshell groups associate well with groupings of particular ostrich bones of the same age that have been found in the region. Abundant eggshells from central and middle Asia are associated with *Struthio asiaticus* Milne-Edwards 1871. Eggshells from the Pliocene of Azerbaijan, West Turkmenia, and, perhaps, Turkey correspond to *S. transcaucasicus* Burchak-Abramovich and Vekua 1971. Numerous eggshell remains from Moldavia and the Ukraine and, perhaps, Hungary (*S. pannonicus* Kretzoi 1953) are associated with ostrich bones that I refer to here as *S. chersonensis* (Brandt 1873).

All ostrich osteological remains from the Pliocene of Europe and Asia are very similar and have been synonymized as *Struthio asiaticus* (Kurochkin, 1970; Kurochkin and Lungu, 1970). However, the eggshell remains mentioned previously are distinct and the features of each "eggshell morphotype species" evolved independently from the Miocene to the Pleistocene (Fig. 22). Because of the apparent stratigraphic, zoogeographic, and paleoecologic value of ostrich eggshell diversity (Mikhailov, 1986, 1988; Mikhailov and Kurochkin, 1988), "eggshell species" need their own names, at least parataxonomic ones. For that reason, the eggshells are considered to be referable to *S. asiaticus, S. transcaucasicus,* and *S. chersonensis.*

The progressive aridity that developed from the late Miocene to the Pleistocene in Eurasia resulted in the disappearance of thick ostrich eggshells with both "aepyornithoid" and "struthioid" pore patterns (*Struthio chersonensis; S. transcaucasicus*) in the late Pliocene to early Pleistocene. In contrast, typically "struthioid" features of thin eggshells evolved step-by-step in the line of the central Asiatic ostrich, *S. asiaticus,* during the Pliocene and into the Holocene. It is noteworthy that Recent *S. camelus* Linnaeus 1758 eggshells, especially those of North African *S. c. camelus,* represent the final evolutionary step in the stratigraphically representative series of the *S. asiaticus* eggshells (Fig. 22). Thus, eggshell remains indicate that Recent *S. camelus* is a direct descendent of the central Asian ostrich lineage, not the East European lineage.

Ostrich eggshells are not found in Asia in deposits earlier than Meotian (Upper Miocene), and the oldest found are referred to

Struthio asiaticus. In Eastern Europe (Moldavia), well-distinguished ostrich eggshells, apparently of a different species, are newly described from the slightly older Sarmatian, and some eggshells are also known from the Meotian–Kimmerian of this region (Mikhailov, 1988). These eggshell fragments as well as osteological remains (Kurochkin and Lungu, 1970) strongly suggest that the specific diversity of *Struthio* in Eastern Europe was greater in the Miocene than in the Pliocene.

In contrast, ostrich eggshell remains are rare in the Miocene of Africa and they are known only from the eastern Mediterranean and western Atlantic (Morocco and Canary Islands; Sauer, 1972; Sauer and Sauer, 1978). Their age is ambiguous, but it may be Pliocene. These eggshells, judging from published photographs, are most similar to the Azerbaijan and Turkey eggshells, or *Struthio transcaucasicus*, but I will refer to them here as the "Mediterranean ostrich." "Aepyornithoid" eggshells of the "Mediterranean ostrich" disappeared before the end of the Pliocene and, with respect to pore patterns, are probably independent of eggshells of the Recent *S. camelus*. Only Pleistocene eggshells [*Psammornis* Andrews 1911 (Sauer, 1969); *Struthio oshanai* Sauer 1966] are known from other regions of the African continent (Lybia, Algiers, southwest Africa). Except for the tibiotarsus fragment of *Eremopezus eocaenus* Andrews 1904 from the Upper Eocene–Lower Oligocene of Egypt, whose systematic position is ambiguous (Sauer, 1969), definite finds of ostrich bones are known in Africa only from Upper Pliocene to lower Pleistocene deposits.

Thus, one can infer that diversity of the genus *Struthio* in the Miocene and Pliocene was apparently greater in Eurasia, especially in Eastern Europe, than in Africa. Moreover, as already mentioned, the Recent African ostrich, *S. camelus*, seems to be a direct descendent of the central Asian ostrich, *S. asiaticus*, which presumably dispersed to Africa in the late Pliocene to early Pleistocene. It can be assumed that at the same time the European ostrich, *S. chersonensis*, just prior to its extinction, also penetrated to Africa. This line later produced the eggshells of *Psammornis rothschildi* Andrews 1911 (Mikhailov and Kurochkin, 1988). One can agree with Sauer (1969:307) that ". . . it might well be, that ratites invaded the Mediterranean basin and Africa in several waves separated by considerable periods of time." Moreover, until the late Tertiary, ostriches in Africa seem to have been restricted to the northern-most parts of the continent, where ostriches arrived from the north and east. All these data on fossil ratite eggshell distribution are in accordance with the hypothesis of a Eurasian origin of ostriches and their subsequent dispersal to Africa (Houde, 1986). They also demonstrate the value of eggshell in biostratigraphy, paleogeographic, and phylogenetic studies and suggest the potential of other fossil eggshells for similar paleontological research.

SUMMARY

Eggshell microstructure can be used to evaluate relationships within the Archosauria, including Aves, because biomineralization of skeletal materials expresses its histogenesis, thereby carrying taxonomic weight. The four general types of sauropsid eggshell are "testudoid" (Chelonia), "crocodiloid" (Crocodilia), "dinosauroid" (Sauropoda, Ornithischia), and "ornithoid" (Aves, Theropoda). On the basis of eggshell microstructure, birds and theropod dinosaurs can be considered as a single branch within the Archosauria, but the monophyletic origin of ratites cannot be demonstrated.

Specific systematic, biostratigraphic, and biogeographic analyses of Eurasian and African ratites demonstrate how eggshell microstructure can be used to trace phylogenetic lineages and possible routes of dispersal. For example, all fossil ratite eggshells support the hypothesis of a Eurasian origin of ostriches and their subsequent dispersal to Africa.

ACKNOWLEDGMENTS

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GIANT FOSSIL EGG FRAGMENT FROM THE TERTIARY OF AUSTRALIA

D. L. G. Williams and P. Vickers-Rich

ABSTRACT. In 1971, the fragment of a very large eggshell was found in Tertiary sediments of northern South Australia. The thickness of this fragment (mean, 4.07 ± 0.05 mm) indicates that the intact egg would have rivaled or surpassed the size of the previously largest known eggs, those of the Malagassy elephant-bird, *Aepyornis*. Although the microstructure of the Australian eggshell fragment is unusual for birds, it is entirely consistent with avian eggs and not of reptilian eggs. Even though no direct association of the eggshell can be made with a specific Australian avian group, the endemic Dromornithidae are the most likely candidates.

Key words: Aves, egg, Australia, Tertiary, Dromornithidae.

INTRODUCTION

The study of fossil eggs provides insights into the taxonomy (Hirsch, 1983; Hirsch and Packard, 1987; Horner, 1982) and nesting biology of species that might otherwise be known only from skeletal remains, or not at all. Fossil eggs are rarely preserved intact, but shell fragments are relatively common and may be locally abundant. Cenozoic deposits in Australia, particularly of Quaternary age, frequently contain eggshell fragments. Very often these came from large birds such as emus or the extinct dromornithids (Williams, 1981).

A most spectacular of Australian eggshell finds was made by Dr. M.O. Woodburne in 1971 at Snake Dam on Mulurinna Station (Maree 1:125,000) southeast of Lake Eyre, northern South Australia. The site is near the Clayton River (University of California, Riverside, Department of Geology Locality RV-7237) to the southwest of Peachawarinna Bore. The eggshell was found "at the base of the bluffs contain[ing] Etadunna Fm. grn [green] claystone" (M.O. Woodburne, field notes, 9 October 1971) that was overlain by a red sandstone and claystone (cf. Tirari Formation) and gypsiferous claystones and sandstones (cf. Katipiri Sands). Fish remains were associated with the eggshell fragment. The find of the Snake Dam eggshell fragment (UCR #17877; see Fig. 1) was significant because of its thickness, which indicated that it was from an egg that rivaled or surpassed that of the largest of the Malagassy elephant-birds, *Aepyornis* spp. Elephant-bird eggs were as large as 35 cm in length and 22 cm in breadth (or width) (Berger et al., 1975; Rahn et al., ms). The single eggshell fragment (Fig. 1; Tables 1, 2) has been analyzed to determine the size of the original egg, the porosity of the shell, and the state of development and to identify its taxonomic origin. The shell structure of the Snake Dam egg is unique in our experience, matched in its unusual structure only by the triple-layered shell of the emus.

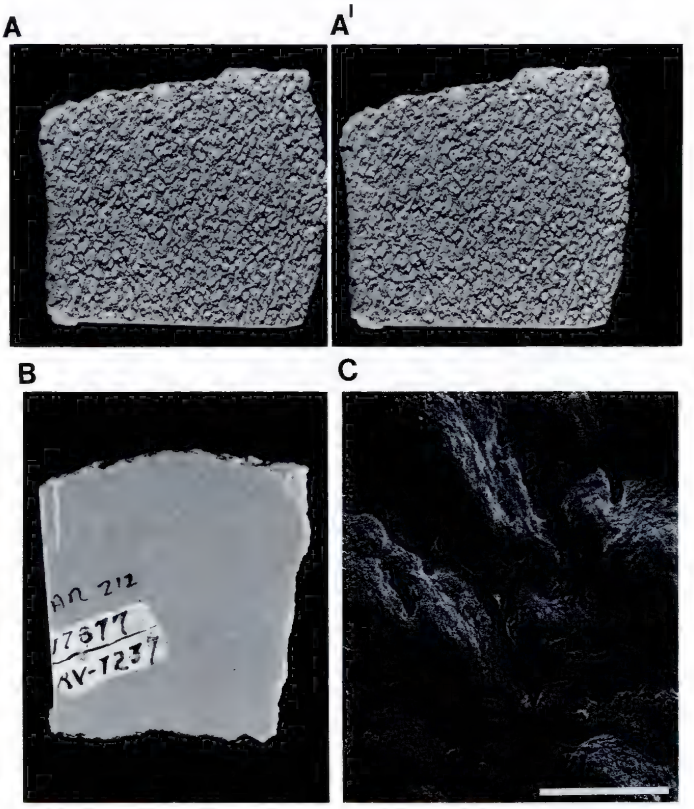

Figure 1. Fragment of a very large Miocene egg [UCR (Univ. Calif. Riverside) 17877, loc. RV-7237] of cf. *Dromornis*, from Snake Dam, Clayton River, South Australia. **A, A'.** Stereo pair of external aspect of shell. **B.** Internal aspect of shell; least width measurement of complete fragment (left margin in illustrations A and A'), 24.9 mm. **C.** Electron micrograph of outer surface of egg; scale bar = 0.60 mm.

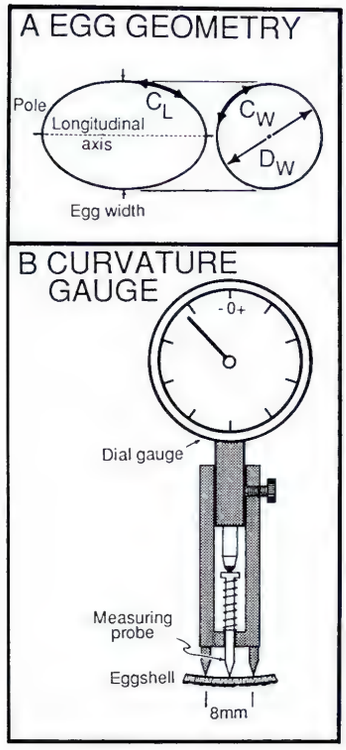

Figure 2. **A.** Egg geometry, showing curvature components C_L, C_W, and egg width, D_W. **B.** Construction of shell curvature gauge.

The analysis was performed using the techniques outlined by Williams et al. (1984) and Williams (1981). It was assumed that the shell fragment available for study was representative of the whole egg and that the physiology of the original egg was comparable to that of modern eggs of large birds.

METHODS

Thickness was measured with vernier calipers, taking the mean of 13 readings. Curvature measurements were made at several points on the smooth inner surface of the shell fragment. The curvature gauge was constructed as described by Williams (1981), and it is a modified Geneva lens measure (see Fig. 2).

A single tangential thin section from about the mid-level of the shell was scored for porosity (Williams et al., 1984). Shell area was estimated by optical enlargement of the thin section using a planimeter. Pore diameters of 38 pores were measured using a calibrated eyepiece fitted to a petrographic microscope. Water vapor conductance of the egg was estimated using data from Ar et al. (1974), as applied by Williams et al. (1984).

Table 1. Characteristics of the Snake Dam fossil shell fragment, cf. *Dromornis* (UCR 17877).

Shell area examined	59.6 mm²
Pore density per mm²	1.7
Mean pore area	3.2 (+2.7/−1.9 mm²) × 10^3
Mean pore size, major axis	79.6 ± 30.2 μ
Mean pore size, minor axis	46.4 ± 14.5 μ
Major axis/minor axis	1.7
% Total pore area	0.54%

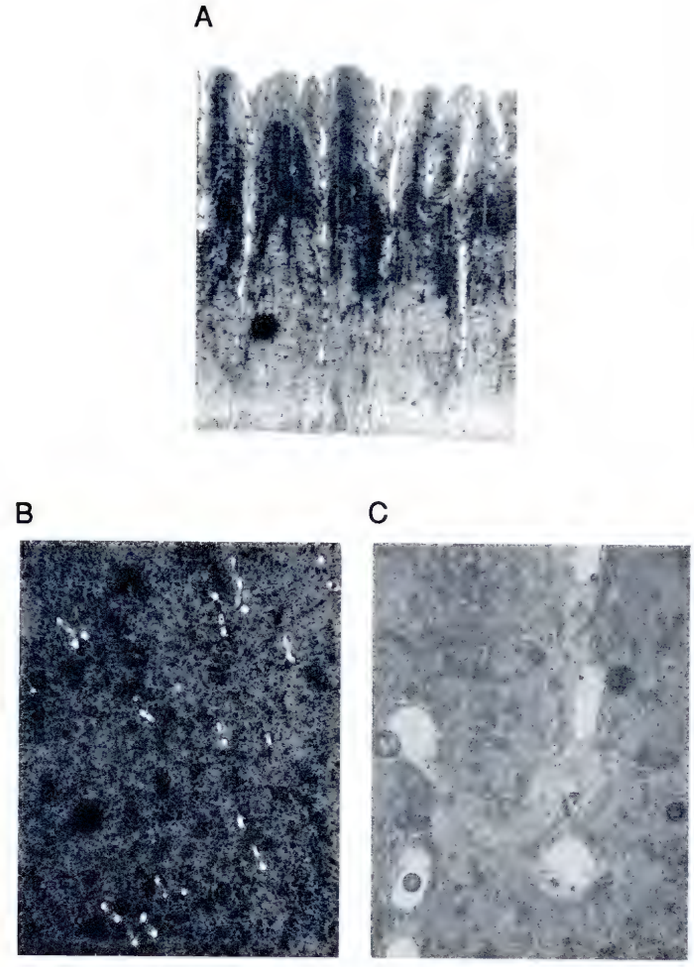

Figure 3. Thin sections of the Snake Dam eggshell fragment (UCR 17877). **A.** Radial section, perpendicular to egg axis. Pores visible as deep fissures. Crystal columns appear narrow in this plane, but they are elongated when viewed parallel to egg axis. **B.** Tangential section about one-third the distance from inner shell surface. Pores occur in linear arrays approximately parallel to the egg axis. **C.** Enlarged view of pores with calcite crystals partially infilling some pores. Shell thickness = 4 mm; mean pore size = 80 microns × 46 microns.

Chemical analysis and X-ray diffraction analysis were performed on a 96-mg sample of the shell.

EGG SIZE

SHELL CURVATURE

Curvature readings give values of egg width as large as 118 mm, including shell thickness. Longitudinal curvature was too small to be measured with the curvature gauge, but the contrast between the two curvature components shows that the fragment does not originate close to the poles of the egg. The fragment is not from the equatorial region, so the value of egg width determined from this approach is a minimum.

SHELL THICKNESS AND ESTIMATED EGG WEIGHT

A mean value of 4.07 ± 0.05 mm was obtained from 13 readings. Using the regression of Ar et al. (1974) based on shell thickness

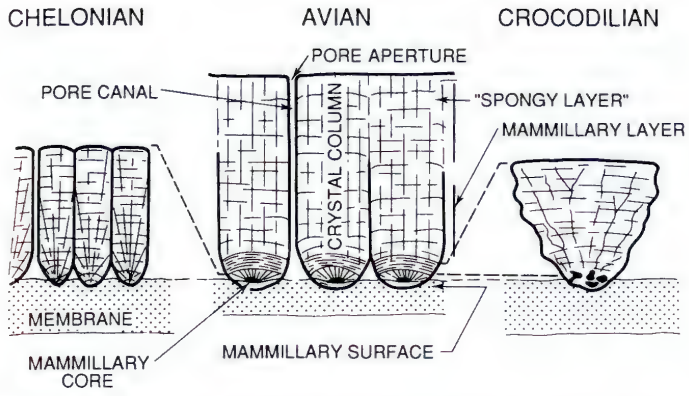

Figure 4. Schematic diagram of vertebrate eggshell, external surface at top (after Hirsch, 1983).

Table 2. Characteristics of the Snake Dam eggshell fragment (UCR 17877) derived from shell properties. *Estimate based on shell porosity, pore length. **Prediction based on egg weight, using fresh bird eggs.

Egg width	240–290 mm
Egg length	300–430 mm
Egg volume	114,700–134,000 mm^3
Egg weight	12,600–14,700 g
Shell thickness	4.07±0.05 mm
Functional pore length (L)	0.38 mm
Egg surface area	25,000–27,800 mm^2
% Pore area	0.535%
Total pore area (Ap)	13.4–14.9 cm^2
*Estimated G_{H_2O}	826–917 mg/torr/day
**Predicted avian G_{H_2O}	683–769 mg/torr/day

(weight = $1.05 \times 10^6 \times$ shell thickness$^{2.19}$), the Snake Dam egg would have weighed 14.7 kg when laid! This would be one of the largest bird eggs known. Ar et al. (1974) used total shell thickness for their regression, which in the case of most shell types is equivalent to functional pore length. However, the Snake Dam shell has a rugose surface, and the pores are effectively only 94 percent of measured shell thickness. If shell thickness is adjusted to 94 percent of 4.07 mm, a value of 3.8 mm is obtained, yielding an estimate of 12.6 kg for an egg weight.

EGG DIMENSIONS (BASED ON SHELL THICKNESS)

Using the estimate 12.6–14.7 kg for egg weight and assuming a possible range of 1.1–1.7 for egg elongation (Hoyt, 1976, 1979), the dimensions of the Snake Dam egg can be calculated as follows: (1) egg elongation = 1.1; for an egg weight of 12.6 kg, 27.3 cm × 30.1 cm; for an egg weight of 14.7 kg, 28.8 cm × 31.7 cm; (2) egg elongation = 1.7; for an egg weight of 12.6 kg, 23.6 cm × 40.2 cm; for an egg weight of 14.7, 24.9 cm × 42.3 cm. This gives a possible size range of 24–29 cm × 30–43 cm for the egg.

SHELL STRUCTURE

The outer surface of the Snake Dam fragment (Figs. 1A, 3B, C) is very unusual for bird eggshell in that it consists of fine ridgelets lying close together, separated by deep fissures. Most bird eggshell has a relatively smooth surface, marked only by tiny pits where the pores communicate to the surface. Curvature analysis shows that the ridgelets on the Snake Dam shell are aligned with the egg axis, which is typical of many egg types bearing elongate surface features. Thin sections show that the shell pores connect with the fissures near the outer shell surface (Fig. 3B, C) Fissuring extends about one-third of the way through the shell, possibly effecting the strength of the egg and the ease with which the chick could have escaped upon hatching.

Tangential sections through the shell reveal that the crystal columns, the basic units that make up the shell, are in close contact via interdigitating boundaries. Both radial and tangential sections, viewed with crossed polars, show that the crystalline structure of the shell is intact.

Radial sections reveal prominent "growth lines" parallel to the shell surface (Fig. 3). These lines are convex outward near the inner shell surface, where they conform to the concentric structure of the mammillary cores. Inclusions such as these "growth lines" are possibly the remains of organic material incorporated during shell growth. The mammillary cores (Figs. 3, 4) are eroded in appearance, suggesting that the Snake Dam egg had been incubated at least to the point of skeletal calcification of the chick (Erben et al., 1979). Pores are rarely solitary, tending to branch into pairs or triplets, and branching occurs parallel to the egg axis.

In no case have blocked pores been observed, and there is no sign of alteration as a result of fossilization. Chemical analysis of a small sample of shell revealed that it consists of low-magnesium calcite with a trace of silica. The composition is $(Ca_{0.99}Mg_{0.11})CO_3$, equivalent to 39.02 percent calcium by weight and 0.27 percent magnesium. It is noted that the host sediment, thought to be Etadunna Formation (Miocene), is likely to be a high-Mg dolomitic claystone, which suggests that little chemical exchange has occurred between shell and sediment.

The structure of the Snake Dam shell, although unusual for bird eggshell, is comparable in its uniqueness with the multilayered shell of the emu. The form of the crystal columns, and their intimate contact with each other, combined with the highly organized branching pore structure are entirely consistent with bird eggshell, but not typical of reptile shell.

SHELL POROSITY

Porosity was measured on one 60-mm tangential section from about the midlevel of the shell. This was a compromise, because the number and size of pores varies at different levels within the shell. The data obtained are, therefore, an approximation of the true value for the egg.

Water vapor conductance is a measure of the potential gas exchange of the whole egg; it relates to the requirements for respiratory gas exchange between embryo and the nest environment. Results obtained from a single shell fragment are only an approximation to the actual value, but the result obtained from porosity data may be checked against regressions based on egg weights, measured for living bird species (Ar et al., 1974).

Using an estimated egg weight of 14.7 kg and an egg density of 1.10 g/cc (Paganelli et al., 1974), egg volume can be calculated. From this, egg surface area can be estimated (Table 2). Applying the relationship $G_{H_2O} = 23.42 \times A_p \times L^1$ (Ar et al., 1974), water vapor conductance would be 917 mg/torr/day (i.e., the amount of water lost per egg per day per torr of partial pressure). Using only the estimated egg weight, a prediction of gas conductance can be obtained for a normal bird egg (above-ground nester) of a given size using the equation $G_{H_2O} = 0.432$

× $W^{0.78}$ (Ar et al., 1974). In this case, a value of 769 mg/torr/day is obtained, which is in good agreement with the first estimate. If egg weight was closer to the lower estimate (12.6 kg), then the corresponding values would be 826 and 683 mg/torr/day, respectively. The two estimates are rather close; if, on the other hand, they differed by a factor of 2 or more, then underground incubation of the eggs would be a distinct possibility (Seymour and Ackerman, 1980; Williams et al., 1984).

SUMMARY

The Snake Dam shell fragment is what remains of an extremely large egg, with an estimated weight of 12–15 kg. Its shell structure, while unusual for bird eggshell, is clearly bird-like. Physiologically, the egg was probably not unusual because its porosity is consistent with above-ground incubation. The shell structure is unlike that of any other bird, and there are no obvious similarities with eggshell of any existing large ground birds in Australia; it does not resemble the eggshell of the only other sizeable bird whose eggs are known in the Australian fossil record, *Genyornis newtoni* Stirling and Zietz 1896. Consequently, no phylogenetic conclusion can be reached from this study. However, the enormous size of the Snake Dam egg is consistent with its tentative attribution to *Dromornis* sp., the largest known fossil bird of the late Cenozoic (Rich, 1979).

ACKNOWLEDGMENTS

Much of the original work on the Snake Dam eggshell was carried out by D.L.G. Williams while he was a research fellow at Australian National University. Tragically, Williams did not have the opportunity to conclude his study of the microanatomy of the eggshell structure because of his untimely death. We wish to thank both ANU and the Monash University for monetary assistance and for providing the facilities allowing completion of this work. We thank M.O. Woodburne for access to his field notes and for allowing us to study the specimen. We also thank I. Stewart, S. Morton, D. Gelt, and P. Hermansen for assistance with photographs, electron micrographs, and word-processing. Karl Hirsch provided a helpful critique of an early draft of this paper.

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MORPHOLOGICAL DIVERGENCE WITHIN THE ORDER APODIFORMES AS REVEALED BY THE STRUCTURE OF THE HUMERUS

Alexandr A. Karkhu

ABSTRACT. The analysis of humeral structure allows the definition of two main groups within the Apodiformes. The orientation of the caput humeri determines the type of mobility and, as a consequence, proportions of the humerus. The Paleogene genera *Aegialornis, Primapus,* and *Cypselavus* and the Recent genus *Hemiprocne* all represent a single trend of specialization, and this provides a basis for uniting them in the family Hemiprocnidae. The Apodidae, including the fossil genera *Procypseloides* and *Scaniacypselus,* the Trochilidae, and the Paleogene family Jungornithidae all possess a totally different structure of the humerus. I here propose a new suborder, Hemiprocni, to reflect the marked differences between the Hemiprocnidae and the families of the suborder Apodi.

Key words: Apodiformes, humerus, morphology.

INTRODUCTION

The Apodiformes (*sensu* Wetmore, 1960) are a highly derived group of birds that possess a very distinctive humerus. Considering that the ability for high-speed maneuvering flight is one of the definitive characters of the Apodiformes, it can be assumed that morphological differences in an element as functionally important as the humerus should provide a good basis for the study of phylogenetic relationships within the order. In the structure of their humerus, true swifts and hummingbirds differ greatly from not only the representatives of other orders, but also from the crested swifts (Hemiprocnidae) and several Paleogene genera similar to them. Fortunately for this type of study, humeri are known for all known fossil species belonging to these groups.

A comparative analysis of humeri in fossil and Recent Apodiformes was undertaken recently by Harrison (1984) and, on a smaller scale, by Peters (1985). Both investigators considered the following features, among others: the relative shortness and width of the humeral shaft, the form and orientation of the crista pectoralis, the size and position of the processus supracondylaris dorsalis, and the presence and position of the tuberculum m. tensor propatagialis, pars brevis. They reached different conclusions, however, concerning the affinities of the Early Eocene *Primapus lacki* Harrison and Walker 1975, which is represented solely by humeri. Harrison (1984) considers this form to be an early representative of apodid specialization and indicated that the genus belonged in a separate subfamily of the Apodidae. Peters (1985), on the other hand, attributes *Primapus* Harrison and Walker 1975 to the Paleogene genus *Aegialornis* Lydekker 1891, which belongs to the hemiprocnid group, in the wide sense, of Apodiformes.

The disagreement over the placement of *Primapus* suggests that some of the features evaluated may not possess the taxonomic and phylogenetic significance ascribed to them. The study of an Early Oligocene apodiform, recently described in the new family Jungornithidae Karhu 1988, provides additional characters diagnostic of either hemiprocnid or apodid specializations within the Apodiformes. The present paper addresses the interrelationships of some of the characteristic features of humeri of apodiforms.

MATERIAL

The discussion of humeral structure in the fossil genera *Aegialornis, Primapus, Cypselavus* Gaillard 1908, *Procypseloides* Harrison 1984, and *Scaniacypselus* Harrison 1984 is based on the published literature (Collins, 1976; Gaillard, 1939; Harrison, 1975, 1984; Harrison and Walker, 1975, 1977; Mourer-Chauviré, 1978; Peters, 1985). The specimen of *Jungornis tesselatus* Karhu 1988 is in the collections of the Paleontological Institute of the USSR Academy of Sciences. The skeletons of *Hemiprocne mystacea* (Lesson 1827) and *H. longipennis* (Rafinesque 1802) were loaned by the Rijksmuseum van Natuurlijke Historie, Leiden. The humerus of *H. comata* (Temminck 1824) was studied on a spirit specimen from the National Museum of Natural History, Smithsonian Institution, Washington, D.C. The material of the five species of true swifts [*Apus apus* (Linnaeus 1758), *A. pacificus* (Latham 1801), *Aeronautes saxatilis* (Woodhouse 1853), *Tachornis phoenicobia* Gosse 1847, *Hirundapus caudacutus* (Latham 1801)] and one species of hummingbird [*Archilocus colubris* (Linnaeus 1758)] come from the Recent osteological collections of the Paleontological Institute.

Eocypselus vincenti Harrison 1984 was excluded from this analysis because its inclusion in the Apodiformes is disputed (Karkhu, 1988).

DIAGNOSTIC CHARACTERS OF THE HEMIPROCNID AND APODID GROUPS

The structure of the humeri of fossil and Recent species of Apodiformes has been subjected to repeated comparative anal-

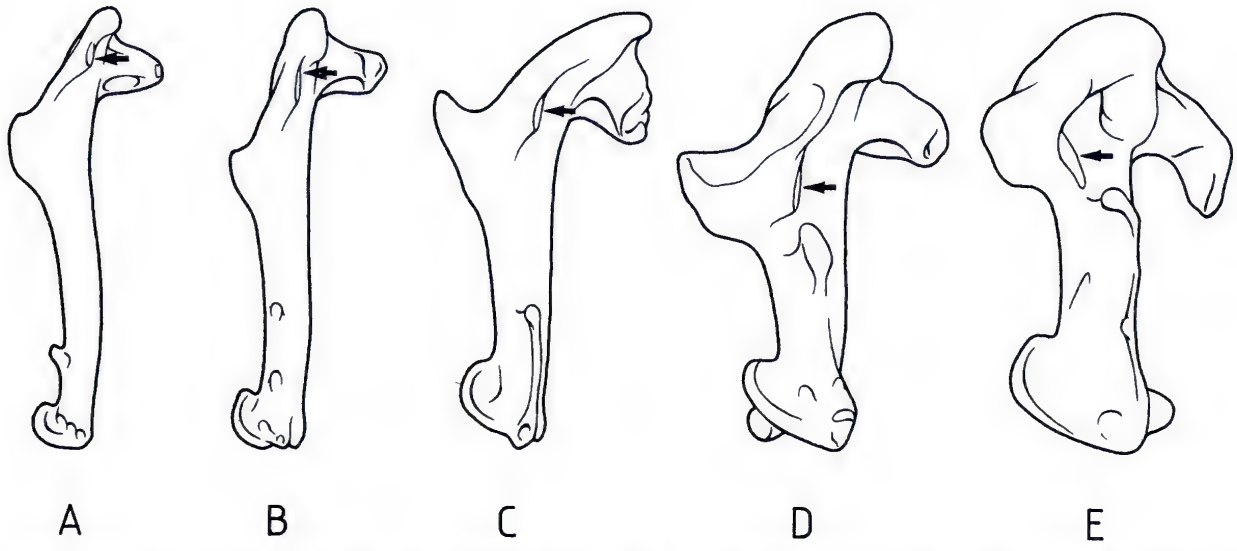

Figure 1. Humeri of Apodiformes standardized for comparison, dorsal view. **A.** *Aegialornis gallicus* (after Collins, 1976). **B.** *Hemiprocne comata.* **C.** *Jungornis tesselatus.* **D.** *Hirundapus caudacutus.* **E.** *Archilocus colubris.*

ysis (e.g., Lowe, 1939; Ballmann, 1976; Collins, 1976; Harrison, 1975, 1984; Mourer-Chauviré, 1978; Zusi and Bentz, 1982; Peters, 1985). Therefore, the general morphological description of this element is omitted and only specific features are discussed below. Anatomical terminology follows Baumel et al. (1979) and Zusi and Bentz (1984). A new term is "distal tubercle of caput humeri."

The Apodiformes can be divided into two groups according to the orientation of the caput humeri. The Paleogene genera *Aegialornis, Primapus,* and *Cypselavus* and the modern crested swifts have an apically directed caput humeri (Fig. 1A, B). The true swifts and the fossil genera *Procypseloides, Scaniacypselus,* and the Early Oligocene *Jungornis* have a caudally directed caput humeri (Fig. 1C, D). Both groups can be clearly defined according to the position of the crista pectoralis and impression m. supracoracoideus. The hemiprocnid group displays the condition typical of most birds; i.e., the impression m. supracoracoideus marks the tuberculum dorsale and lies considerably proximal to the base of the crista pectoralis. In the apodid group, this impression is displaced distad to the level of the base of the crista pectoralis.

The hummingbirds, family Trochilidae, like the members of the apodid group, possess caudally oriented caput humeri and have the impression m. supracoracoideus on the same level with the crista pectoralis (Fig. 1E). An important, distinctive character of hummingbirds is the presence of a well-developed distal tubercle of caput humeri on the caudal surface (Fig. 2D). In the Hemiprocnidae and the Apodidae, the caput humeri has a well-outlined distal border and lacks any such tubercle (Fig. 2A, B). Among fossil forms, only *Jungornis* possesses a small, but still well-defined, tubercle on the caudal surface of the caput humeri (Fig. 2C).

GENERAL PROPORTIONS OF HUMERI IN THE HEMIPROCNID AND APODID GROUPS

For a formal generalized description of humeral proportions, the indices of relative widths of the proximal and distal epiphyses may be used. The width of the proximal epiphysis was measured as the distance from the dorsal surface of the tuberculum dorsale to the ventral surface of the crista bicipitalis. The width of the distal epiphysis was established on the level of the epicondyli.

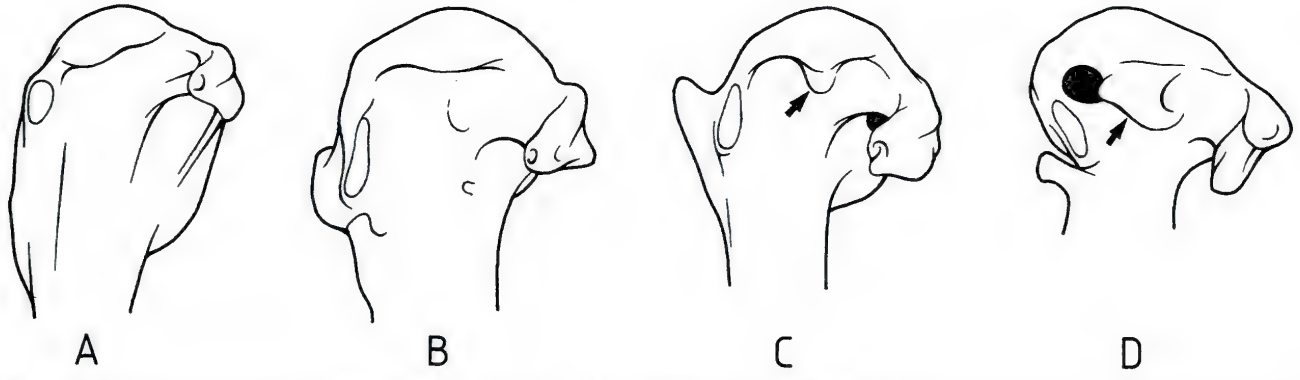

Figure 2. Proximal part of humeri of Apodiformes, caudal view. **A.** *Hemiprocne comata.* **B.** *Hirundapus caudacutus.* **C.** *Jungornis tesselatus.* **D.** *Archilocus colubris.* Arrow indicates distal tubercle of caput humeri.

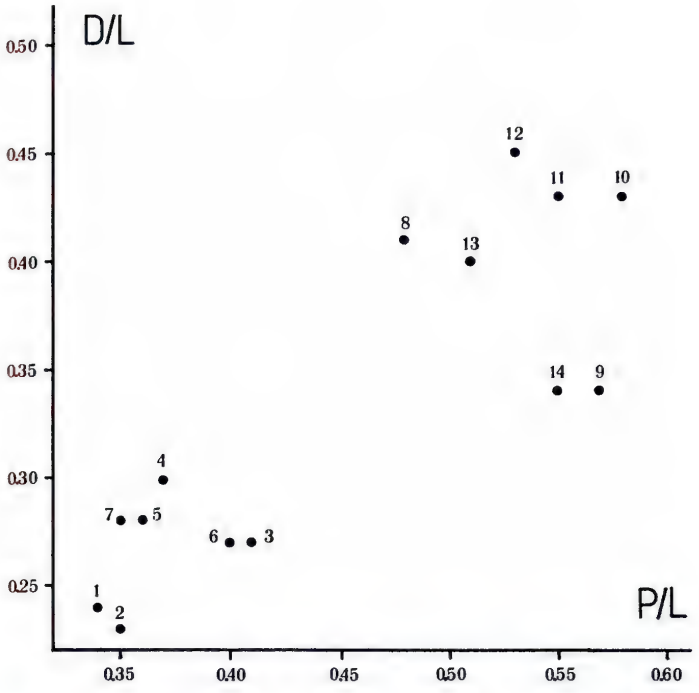

Figure 3. Diagram for the humeral proportions of Apodiformes. **D/L,** the ratio of width of distal epiphysis to total length; **P/L,** the ratio of width of proximal epiphysis to total length. **1.** *Aegialornis gallicus* (after Collins, 1976; Harrison, 1975, 1984). **2.** *Aegialornis wetmorei* (after Collins, 1976; Harrison, 1984). **3.** *Primapus lacki* (after Harrison and Walker, 1975, 1977; Harrison, 1984). **4.** *Cypselavus gallicus* (after Mourer-Chauviré, 1978; Harrison, 1984). **5.** *Hemiprocne mystacea.* **6.** *Hemiprocne longipennis.* **7.** *Hemiprocne comata.* **8.** *Jungornis tesselatus.* **9.** *Cypseloides niger* (after Harrison, 1984). **10.** *Apus apus.* **11.** *Apus pacificus.* **12.** *Tachornis phoenicobia.* **13.** *Aeronautes saxatilis.* **14.** *Hirundapus caudacutus.*

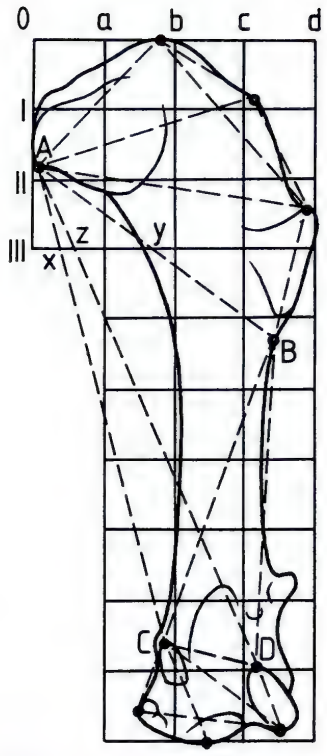

Figure 4. Standard humerus (*Aegialornis gallicus*) of Fig. 5 showing grid lines (solid), landmarks (solid circles), landmark lines (dotted) and functional regions (separated by lines AB and CD). See text for explanation.

The widths of the proximal and distal epiphyses were taken in relation to the total length of the bone.

In the resulting plot of humeral proportions, two isolated groups of points stand out. One corresponds to the representatives of the fossil genera *Aegialornis, Primapus,* and *Cypselavus* and of the Recent genus *Hemiprocne* (Fig. 3, points 1–7). The other group includes the Oligocene *Jungornis* and species of the Apodidae (Fig. 3, points 8–14).

Inadequate data on hummingbirds prevented their inclusion in the diagram. Still, the analysis of the accessible humeral material revealed that they greatly exceed the true swifts in the relative width of the proximal epiphysis.

ANALYSIS OF HUMERAL PATTERN

METHODOLOGY

Data on the relative width of the epiphyses represent only a general aspect of humeral proportions. Discussions of the details of evolution of different parts of the bone and their spatial relationships require special approaches. One such approach is the method of "deformed coordinates." The method proposed here limits subjectivity mainly to the choice of landmarks, or features (Fig. 4). To be chosen as a landmark, a feature must meet the following requirements: (1) possess morphological significance, (2) be identifiable in all of the members of the series under discussion, and (3) lack extreme intrataxon variation. A careful choice of landmarks is essential to a successful analysis of deformed coordinates.

The method of deformed coordinates requires the following steps:

1. Determine limits of functional regions of the humerus; in this case, they are the shaft (diaphysis) and proximal and distal articular regions (epiphyses). The limits are not exact, and are here regarded as lines A–B and C–D in Fig. 4.
2. Superimpose a rectangular grid on the humerus to be used as a standard (*Aegialornis gallicus* in Fig. 4). The shape and complexity of the grid can be determined by practical considerations.
3. Connect landmarks of the standard humerus by straight lines within, but not across, functional regions (Fig. 4). The number of such connections is arbitrary; it should be sufficient to permit formation of deformed grids, but not so large as to require excessive and redundant calculations.
4. The points at which landmark lines cross grid lines are the derived points of the standard humerus. Calculate the ratio of each section (between two successive derived points) to the full length of each landmark line.
5. Connect the landmarks of other humeri in a similar manner and divide the lines into sections in the same proportions as in the standard humerus.
6. Make a deformed grid by connecting the calculated derived points that occur along each grid line (as seen in the standard humerus).

To complete a portion of the grid that lies outside the grid

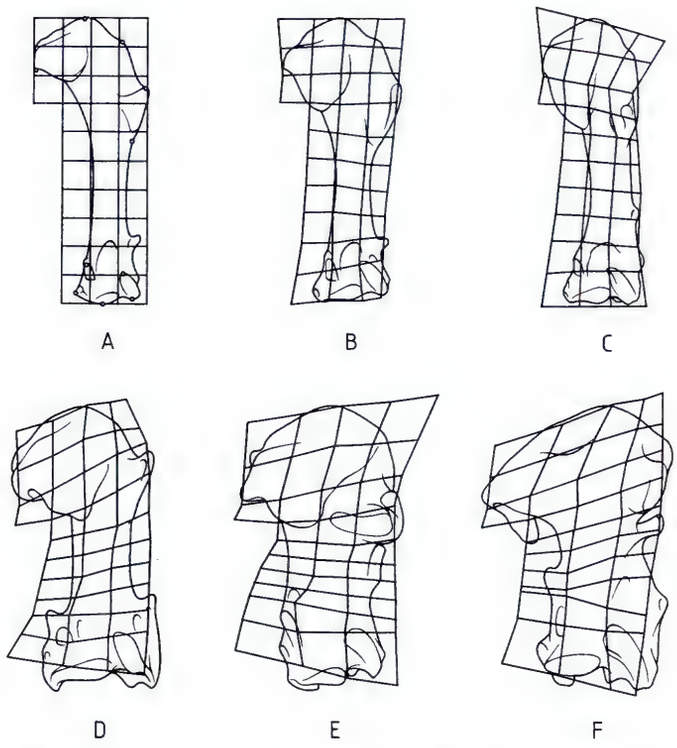

Figure 5. Deformed coordinates, cranial view, based on rectangular grid of *Aegialornis gallicus* (**A**). Landmarks are shown by small circles on *A. gallicus*. **B.** *Primapus lacki*. **C.** *Hemiprocne comata*. **D.** *Jungornis tesselatus*. **E.** *Hirundapus caudacutus*. **F.** *Archilocus colubris*.

formed by step 6 (e.g., point III), determine the ratio of o–x to x–a on grid line III of the standard humerus. On the deformed grid, draw a straight line through y and x of line III and extend it to the left; establish point III using the same ratio as in the standard humerus. Extending line y–x rather than z–x serves to smooth the angle $xa_{III}y$.

In the deformed grid, "horizontal" lines between successive "vertical" ones may have one or more angles depending on the positions of the derived points as described above. In such cases, the grid may be simplified by drawing a single line between the intersections with successive vertical grid lines. The same modification may be made on angled, vertical lines between successive horizontal ones.

The deformation of the grid is provoked by changes in the relative position of landmarks. Transformation, or evolution, of structures that do not carry landmarks has no influence on the deformation of the grid, but it can still be easily determined by the changes in their positions inside the latter.

The most generalized representative of the group studied is chosen as the standard. This permits the interpretation of detected differences as results of progressive morphological specialization. *Aegialornis gallicus* Lydekker 1891 was chosen as the standard for comparison of the Paleogene *Primapus lacki* and *Jungornis tesselatus* and Recent representatives of Hemiprocnidae, Apodidae, and Trochilidae. *Jungornis* was chosen as the standard for the comparison between the true swifts and the hummingbirds because, being a relatively generalized form, it shares some features with both of them. The humeri of all of the forms compared in these analyses were represented by cranial projections of standard length.

DERIVATIVES OF THE RECTANGULAR GRID OF *AEGIALORNIS GALLICUS*

The grid derived for *Primapus lacki* is the least altered (Fig. 5B). The minimal distortions observed in the zones of the proximal epiphysis and the diaphysis are of an irregular nature. A notable deformation occurs only in the region of the condyles, where the distal epiphysis is wider ventrally and longer in the dorsal part. The distal displacement of the crista bicipitalis margin relative to the grid is clear and gives the impression of a shortened diaphysis. Also, in *Primapus* the processus supracondylaris dorsalis is positioned more distad than in *Aegialornis*.

For *Hemiprocne comata* (Fig. 5C), the grid area corresponding to the distal epiphysis and diaphysis generally resembles the pattern in *Primapus* but differs in the lack of lengthening in the region of the condylus dorsalis. The processus supracondylaris dorsalis is positioned more proximad relative to the grid. Considerable grid distortion in the proximal zone results from a cranial turn of the crista pectoralis. The border of the crista bicipitalis is positioned even farther distally than in *Primapus*.

The grid patterns of *Jungornis, Hirundapus,* and *Archilocus* are distinctly different from those of *Primapus* and *Hemiprocne* (Fig. 5D–F). The common features of the former lie in the transverse widening of the grid in the region of the proximal epiphysis, the shortening of the diaphysial zone, and the relative lengthening of the condylar part of the distal epiphysis. The degree of expression of these characters increases in the sequence from *Jungornis* through *Hirundapus* to *Archilocus*. In true swifts and hummingbirds, the diaphysial borders of the humerus are displaced toward the periphery of the grid. In *Jungornis,* the diaphysis remains relatively narrow and the processus supracondylaris dorsalis is on the same level as in *Aegialornis*. In *Jungornis* and *Archilocus,* the broad crest on the dorsal surface of the distal part extends beyond the limits of the grid. In *Archilocus,* the tuberculum m. pronator superficialis occupies a more proximal position than in *Jungornis*. In *Jungornis* and *Hirundapus,* the progressively developed processus flexorius lies outside of the grid, together with the adjoining part of the condylus ventralis. In *Archilocus* the distal protrusion of the processus flexorius is not as strongly developed.

DERIVATIVES OF RECTANGULAR GRID OF *JUNGORNIS TESSELATUS*

When *Hirundapus* and *Archilocus* are compared using the grid of *Aegialornis* as the standard, an overall similar pattern of deformation exists. But when the grid of *Jungornis* is used as an initial object, then their grids are quite different (Fig. 6B, C). The difference is most obvious in the pattern of the proximal epiphysial zone. In *Hirundapus,* the deformation of this region can be interpreted as a consequence of the proximal epiphysis being rotated into the frontal plane with a distal displacement of the crista pectoralis. Additional distortion is also caused by the extension of the dorsal part of the caput humeri. In *Archilocus,* the asymmetric transverse extension of the proximal epiphysial zone is primarily related to the widening of the ventral part of the epiphysis in the region of the crista bicipitalis margin, while the general orientation of the bone axis remains unchanged. In *Hirundapus,* the processus flexorius and the adjoining part of the condylus ventralis lie distal to the limits of the grid, as was observed with the comparison with *Aegialornis*. In both *Hirundapus* and *Archilocus,* the processus supracondylaris dorsalis occupies a much more proximal position relative to that in *Jungornis*.

DISCUSSION

The three independent approaches to structural analysis of the humerus revealed two main groups within the Apodiformes. The first group includes the Paleogene genera *Aegialornis, Primapus,* and *Cypselavus* and the modern crested swifts of the genus *Hemiprocne.* In all of these forms, the caput humeri is directed apically, the impression of m. supracoracoideus lies proximal to the crista pectoralis base, and the diaphysis is relatively long. The second group includes the families Apodidae and Trochilidae as well as the fossil family Jungornithidae. This group is distinguished by the caudal orientation of the caput humeri, the distal displacement of the impression of m. supracoracoideus toward the level of crista pectoralis base, and the shortened proportions of the bone brought about by the decrease in the length of the diaphysis.

Of all the characters of the two apodiform groups, the orientation of the caput humeri is especially important. The orientation is related to the degree of humeral abduction in the spread wing, in that the more caudally oriented the caput humeri, the less the degree of humeral abduction. Or, in other words, the angle with the lateral side of the body is less. The decrease in humeral abduction leads to a concentration of wing mass near the humeral joint. Thus, the inertia moment of the moving wing decreases, and this undoubtedly favors intensive flapping flight. The partial shortening of the wing caused by the decrease in humeral abduction and the corresponding decrease in the arc of motion of the humero-ulnar joint may, in small-sized birds, be easily compensated for by the lengthening of the primaries.

In a flapping wing, the humerus simultaneously performs oscillatory and rotative movements. The rise of the wing is accompanied by supination of the humerus and the lowering of the wing is accompanied by pronation. The degree to which both forms of movement are expressed depends on numerous conditions, but, on the whole, it may be considered that the importance of the rotational component increases with the decrease in humeral abduction. A wing with weak abduction and strong rotation can realize the necessary angular amplitude of flight strokes with less linear displacement of the elbow joint. The decrease in linear amplitude at the distal end of the humerus may lead to shortening of the humeral diaphysis. In the Apodiformes, the caudal orientation of the caput humeri is accompanied by a shortened diaphysis in all cases. The general proportions of the humerus and the transformation pattern typifies an apodiform group comprising the Jungornithidae, Apodidae, and Trochilidae. All of these families feature a caudally oriented caput humeri.

While the functional significance of the orientation of the caput humeri is clear enough, the changes in the relative position of the impression of m. supracoracoideus and the crista pectoralis still cannot be interpreted satisfactorily. However, it may be assumed that the leveling of the attachments of m. pectoralis and the progressively developed m. supracoracoideus are connected with the symmetrical loading of the humeral joint in the course of pronation and supination. Indirect support for this assumption can be found in the related differences in the position of the caput humeri (Fig. 2). In *Jungornis,* true swifts, and hummingbirds, the caput humeri forms a right angle with the long axis of the bone. In representatives of the hemiprocnid group, the ventral part of the caput humeri occupies a more proximal position than the dorsal part.

For the most part, species of the Apodiformes possess a ventrally widened distal epiphysis, the Paleogene *Aegialornis* being the only exception. The widening of the distal epiphysis is related

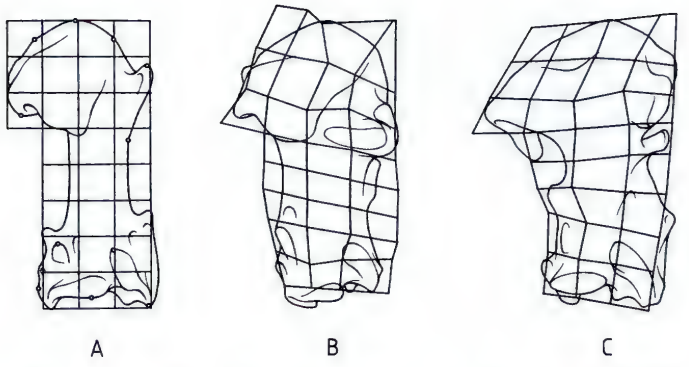

Figure 6. Deformed coordinates, cranial view, based on rectangular grid of *Jungornis tesselatus* (**A**), for humeri of *Hirundapus caudacutus* (**B**) and *Archilocus colubris* (**C**). Landmarks are shown by small circles on *Jungornis.*

to the enlargement of the condylus ventralis. The increase of the articular surface between the humerus and ulna obviously represents a reaction to the growing load in the elbow joint.

The humerus of *Jungornis* possesses some features that are characteristic of true swifts and others characteristic of hummingbirds. The presence of a well-developed apodid-like crista pectoralis is accompanied by a distal tubercle of the caput humeri on the caudal surface, which in the more derived state is characteristic of hummingbirds. The presence in *Jungornis* and hummingbirds of a well-developed tuberculum m. pronator superficialis, although somewhat displaced distad, and a broad crest on the dorsal surface that extends proximad to the processus supracondylaris dorsalis, may have less phylogenetic significance.

Some particularities of *Jungornis* that separate it from hummingbirds resemble those in the true swifts. These features are the structure of the tuberculum ventrale of the proximal epiphysis, the presence of a ventrally projecting tuberculum supracondylare ventrale, and the distinct dorsal border of intumescentia. Such a combination of features is best explained if the three named families shared a common ancestor and some of the features evolved in parallel. Thus, the analysis of humeral structure and the data on *Jungornis* support a hypothesis of affinity between the Apodidae and the Trochilidae.

These comparisons demonstrate that the observed differences between *Aegialornis* and *Hemiprocne* are less than what are usually taken as familial characters within the Apodiformes. The inclusion of *Aegialornis* as a separate subfamily within the Hemiprocnidae is justified. The possibility of such an assignment was outlined earlier by Harrison (1984).

Primapus lacki (Harrison and Walker, 1975) appears to be correctly identified as a representative of the hemiprocnid group. The separate morphological features and the humeral proportions all support that conclusion. Within the hemiprocnid group, *Primapus* is the closest to *Aegialornis,* as indicated by the distal position of the peg-like processus supracondylaris dorsalis, the dorsocranial orientation of the crista pectoralis, and the absence of a prominent attachment tubercle for the m. tensor propatagialis, pars brevis. These similarities led Peters (1985) to consider *Primapus* as a synonym of *Aegialornis.* However, *Primapus* clearly displays some more derived features, including the distal displacement of the crista bicipitalis margin, the widening of the condylus ventralis, and the proximal lengthening of the condylus dorsalis. The similarities and differences deter-

mined for *Primapus* and *Aegialornis* can be reflected taxonomically by retaining the generic status of *Primapus* and including it in the subfamily Aegialornithinae.

The generalized structure of the sternum and shoulder girdle elements suggests that *Jungornis tesselatus* of the Early Oligocene is a relatively unspecialized form (Karkhu, 1988). At the same time, the humerus of *Jungornis* possesses a number of characters that resemble those of the true swifts and hummingbirds. This suggests that morphological specialization of the apodiform humerus occurred in the early stages of apodiform radiation. The oldest documented evidence of hemiprocnid and apodid divergence appears in the Early Eocene with *Primapus* and Middle Eocene with *Scaniacypselus* (Harrison, 1984). The distinctive characters within these evolutionary lines are to be found in the structure of the humerus, as well as in other features of the morphology and biology of fossil and Recent representatives of the Hemiprocnidae and Apodidae.

The inclusion of the Hemiprocnidae and Apodidae in one suborder is contradictory to the evidence for their long, independent evolution, which has brought about a whole suite of complex features. The separation of the Hemiprocnidae from the suborder Apodi and the erection of a new suborder, Hemiprocni, for the family is justified to reflect the high degree of differentiation between these families.

An analysis of the relationships of the families Jungornithidae, Apodidae, and Trochilidae lies beyond the limits of the present paper. A partial analysis of these families was presented by Karkhu (1988).

SUMMARY

The specialization of the humerus within the Apodiformes has occurred along two main directions since at least the Early to Middle Eocene. These trends are distinguished from one another by the orientation of the caput humeri and the degree of shortness of the diaphysis, these two characters being functionally connected. From this viewpoint, the Hemiprocnidae and the Apodidae belong to different lines that diverged from the apodiform basal stock, a conclusion that prevents their being united within the suborder Apodi. The Hemiprocnidae deserve to be distinguished in their own separate suborder, the Hemiprocni.

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LIGHT BONES IN BIRDS

Paul Bühler

ABSTRACT. Recent flying birds have various weight-reducing adaptations of the skeleton, including (1) constructions comprising flat bony bars, (2) fusion of "individual" bones, (3) reduction of teeth, (4) bones comprising hollow tubes, (5) sandwich constructions, (6) substitution of air for marrow in long bones and sandwich bones, (7) strengthening of thin layers of bone with an outer and an inner covering of collagenous fibers, and (8) bony bending zones, including plate-spring articulations, within the jaws and palate. The skeleton of the London specimen of *Archaeopteryx* and the vertebrae and long bones of several theropods were studied to determine when some of these features originated in the evolution of birds. *Archaeopteryx* has hollow bones with thin walls, the relative thicknesses of which are within the range of variation of modern birds. Parts of the braincase of *Archaeopteryx* are pneumatized. Relatively thin-walled long bones and bird-like pneumatization in the vertebrae had evolved in non-flying theropods. Thus, some lightweight features of bones seen in birds must have evolved before birds.

KURZFASSUNG. Im Skelett rezenter Vögel sind verschiedene Leichtbau-Anpassungen ausgebildet: (1) Flachstabknochen als Teile z.B. des Brustkorbs; (2) Verschmelzung von Einzelknochen; (3) Rückbildung der Zähne; (4) dünnwandige Röhrenknochen; (5) Knochensandwich mit zwischengeschalteter Spongiosa; (6) Pneumatisation von Röhrenknochen und Sandwichstrukturen; (7) Bindegewebe als äussere und innere Deckschicht dünner Knochenplatten; (8) Blattfeder-Gelenkung im Kiefer-Gaumenapparat. Um zu klären, wann derartige Anpassungen entstanden sind, wurde der Londoner *Archaeopteryx* und Wirbel und Röhrenknochen theropoder Dinosaurier vergleichend untersucht: Bei *Archaeopteryx* sind Röhrenknochen ausgebildet, deren Wandungen so dünn sind, dass die relative Wandungsdicke im Variationsbereich moderner Vögel liegt. Teile der Schädelkapsel von *Archaeopteryx* sind pneumatisierte Sandwichstrukturen. Bei den flugunfähigen Theropoden sind relativ dünnwandige Röhrenknochen und pneumatisierte Wirbel ausgebildet. Daraus ergibt sich, dass ein Teil der Leichbaustrukturen des Vogelskeletts älter sind als die Vögel selbst.

Key words: *Archaeopteryx*, Aves, birds, bone structure, lightweight, mechanical efficiency, minimum mass, osteology.

INTRODUCTION

Recent flying birds have characteristic and very efficient weight-reducing skeletal adaptations, such as thin-walled long bones and air-filled sandwich structure of the skull walls. These adaptations are only a part of a broader spectrum of transformations that are the result of selection for weight reduction in the avian skeleton. This evolutionary trend began when the first tetrapods left the aquatic environment and lost the buoyancy effect of water. On the other hand, many lightweight structures of birds are so distinctive that it seems probable that they were first developed during the evolutionary origin of birds from their reptilian ancestors. The major reason underlying the development of lightweight skeletal structures in birds and other flying vertebrates such as pterosaurs, as well as in oversized walking animals such as elephants and dinosaurs, is that bony tissue, contrary to widely held views, is a comparatively poor lightweight material. The calcium salts component of bone that provides its strength against compressive forces is relatively heavy and it has relatively low strength against certain types of forces (Currey, 1984).

The basic problem is that most forces acting on the individual elements of the vertebrate skeleton are asymmetrical, resulting in bending moments on the bones and a very uneven distribution of stresses within the skeletal element. These stresses lie in the same plane as the impacting forces with the maximum stresses in the periphery of the object and dropping off rapidly to a neutral zone of no stress in the interior. Relative to their weight, solid bones have low strength to resist these asymmetrical bending forces because much of the bony material is resisting little stress. Efficient supporting elements to withstand bending forces are constructed according to a maximum–minimum principle, or maximum strength of the supporting element for minimum weight. The general solution is to place the resisting material in the periphery of the supporting element and as far from its center as possible. Sufficient interconnecting struts connect the peripheral material to keep the entire element rigid.

Tetrapods, and especially flying forms such as birds and pterosaurs, have evolved the same types of lightweight structures in their bony skeleton as used by engineers in the construction of large buildings and bridges, in which strength must be balanced against the weight of the construction. This paper is an overview of the diversity of skeletal lightweight structures in extant birds (Bühler, 1972, 1986) and an attempt to develop some ideas about the origin of these skeletal adaptations based on an analysis of *Archaeopteryx* von Meyer 1861 and a sample of dinosaur fossils.

STRUCTURES

FLAT BARS

Within the avian skeleton, flat bony bars or bony rods represent one of several different lightweight principles or strategies. Flat-

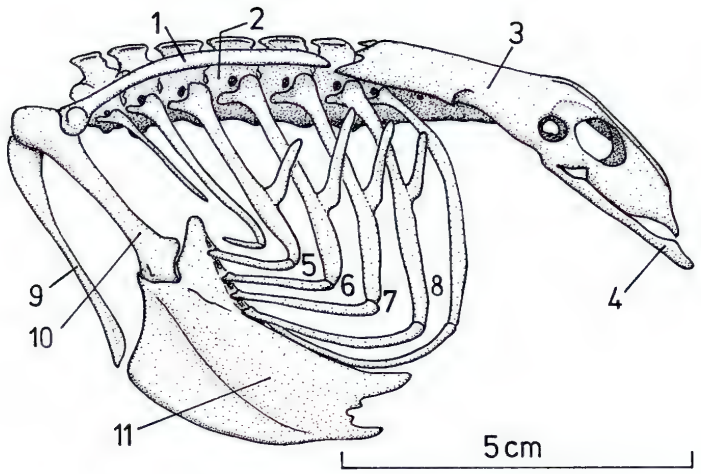

Figure 1. Flat bony bars within the splint basket construction of the body skeleton of a Barn Owl (*Tyto alba*). **1,** Scapular blade; **2,** vertebral column (not flattened; with pneumatic pores); **3, 4,** pelvis; **5–8,** ribs; **9–11** (including 1), shoulder girdle.

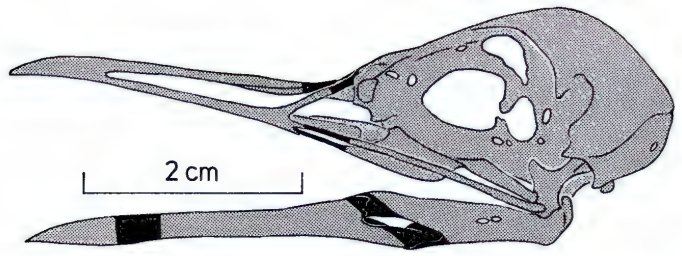

Figure 2. Flat bony bars within the framework of the jaw apparatus of a Little Gull (*Larus minutus*). Shaded black area, plate-spring articulations or bending zones.

tened bones play a special role in the avian rib cage (Fig. 1) and in the jaw apparatus within the order Charadriiformes and many other groups (Fig. 2). In some cases, the flat bar has a T-shaped or an I-shaped cross-section, similar to the weight-reducing beams used in architectural constructions. These bony bars are flattened so that their maximum dimension is in the same plane as that of the deforming force; hence, bony material is placed far from the center of the supporting element.

FUSION OF BONES

An important weight-reducing mechanism in birds is to fuse individual bones to reduce sutures, as for example in the skull and in the synsacrum and pelvic girdle. Sutures are the gaps between centers of ossification that house growth tissue and allow the adjacent bones to extend steadily. They are strengthened by collagen fibers, by the thickening of the bony contact walls, and/or by a meandering shape (Fig. 3), which means that they are strengthened by additional material because of the increased area of contact. Because sutures function as growth zones, extensive fusion is only possible in birds with a short growing phase, as in most Recent birds with parental care in which the young birds reach their adult size within weeks or a few months.

One advantage of fusion is to save material that would be necessary to prevent sutures from breakage or that would be necessary to hold the bones in position (e.g., muscles). In reptiles and some mammals (e.g., cetaceans and microtids), early birds (*Archaeopteryx*, *Hesperornis* Marsh 1872, and *Parahesperornis* Martin 1983; Bühler, 1987), and, to some extent, paleognathous birds, the sutures of the skull are open during the whole life time of the animal.

Another advantage of fusion is that it results in larger bony units, such as the braincase and the pelvic complex, which can be constructed in a force-resisting shape with relatively little material. In some textbooks, one can find the statement that the fusion of avian bones is a by-product of pneumatization. That this is not the case is shown by the fact that many non-pneumatized bones, e.g., the individual elements of the tarsometatarsus, are fused in all extant birds. Weight-reducing fusion of bones also evolved in the flying pterosaurs (Wellnhofer, 1978), which indicates that these reptiles must have had a short growing phase, probably with parental care.

LOSS OF TEETH

The reduction of teeth and their replacement by horny sheaths in birds also appears to be a weight-reducing transformation, even though it does not involve the skeleton in a narrow sense. It is of interest that some pterosaurs also lost their teeth and evolved horny coverings of the jaws convergently (Wellnhofer, 1978). However, one should keep in mind that turtles and a number of extinct groups of reptiles have also lost their teeth and evolved comparable horny sheaths of the jaws without any obvious need to reduce weight. In birds, the evolutionary reduction and final loss of teeth is very poorly documented. The only well-known intermediate stage is represented by *Hesperornis* and the similar *Parahesperornis* (Gingerich, 1976; Martin, 1984), in which the teeth of the premaxilla are lost (Fig. 4). The ancestors of the hesperornithids probably had reduced the teeth of the premaxilla before they lost the ability to fly, i.e., before they began to live as divers.

Weight reduction in birds by the loss of teeth requires some additional explanation because the flying bats and many pterosaurs have retained their teeth. Loss of teeth in birds may well have resulted from a combination of obligatory homoiothermy and their long necks. Obligatory homoiothermy in birds and mammals requires a high metabolic level, which depends on rapid digestion. Initial mechanical decomposition of food is necessary for rapid digestion, which is accomplished by chewing in mammals and by the muscular gizzard in birds. Chewing requires teeth, heavy-boned jaws (the bone in toothed jaws is relatively dense because of the constant forces exerted on it) and large jaw muscles. If these heavy structures are placed at the end of a long neck, as possessed by birds, a large torque or moment results because of the long moment arm formed by the long neck. Hence, larger cervical muscles are needed to hold the neck and head in position, all of which adds to the weight of the animal. Note that it is a weight-reducing feature of birds to concentrate the mass of all appendages—the neck and head, the wings, the legs, and the tail—close to the body trunk, which reduces the torque of these structures and, hence, the muscular force needed to move these appendages relative to the trunk, thereby increasing skeletal efficiency. In the same way, the loss of teeth in birds and their functional replacement by the gizzard results in a lighter skeleton.

Retention of teeth in bats may be because these mammals have a short neck, hence the head is close to the trunk and the

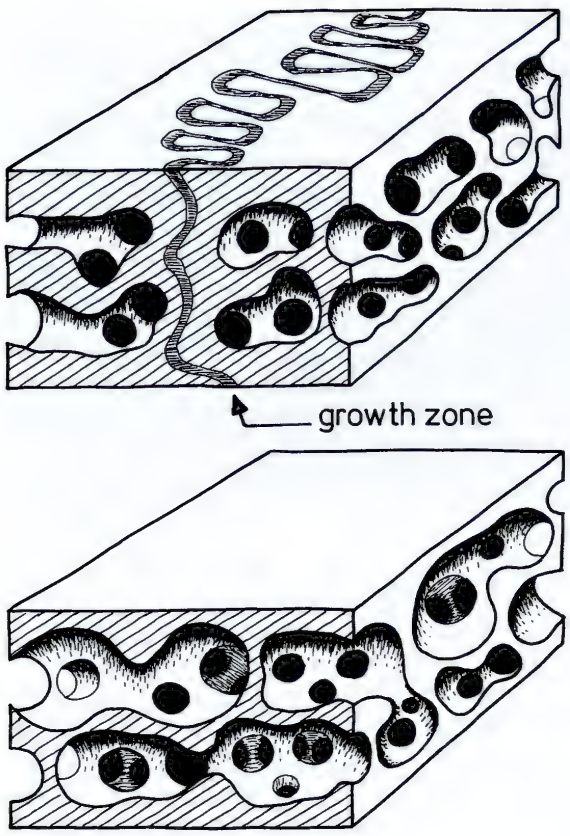

Figure 3. Above: bone suture with growth zone of connective tissue (diagrammatic); below: seamless merging of two bones.

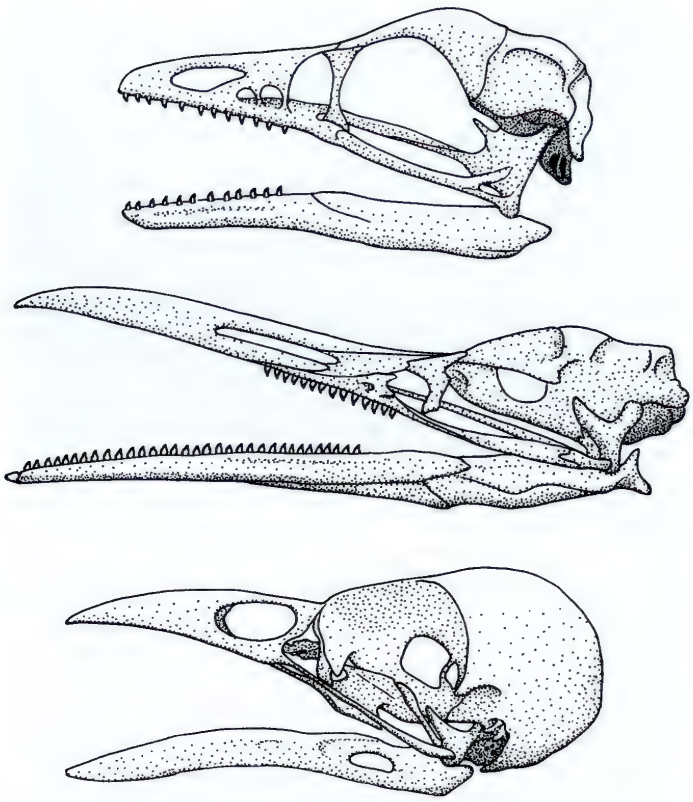

Figure 4. *Hesperornis* (center) as the only well-known intermediate stage of the avian reduction of teeth. Above: *Archaeopteryx;* below: *Corvus* (as an example of a modern bird).

weight of the chewing apparatus does not result in a large torque. Moreover, teeth cannot be lost without the evolution of a substitute mechanical grinding structure for foods; a muscular stomach has apparently not evolved in mammals.

HOLLOW TUBULAR BONES

Another weight-reducing feature realized in the skeleton of birds is the hollow tube comprising the middle segment of the long bones. This feature is, however, found in the long bones of all tetrapods. The cavity of these hollow bones is filled with either marrow or air contained within air sacs. Thus, contrary to a widespread misunderstanding, hollow bones do not at all depend upon pneumatization, which must be examined separately.

The formation of a more or less thin wall is the crucial detail of the lightweight tubular bone, a well-known fact in engineering. Birds differ from most other tetrapods not in the possession of hollow bones, but in the fact that the walls of their hollow bones are very thin. Currey and Alexander (1985) claimed that the relative thickness of the tubular wall of avian long bones is not correlated to body size in flying birds. Their results are surprising if one considers that volume and weight of the body increases in three dimensions (the cube of the linear dimension), whereas the weight-bearing wing surface increases only in two dimensions (the square of the linear dimension), if the general size of the bird is increasing and the proportions are kept constant (cf. Slijper, 1967; McMahon and Bonner, 1983; Calder, 1984; Schmidt-Nielsen, 1984). This relationship may not be of great constructional importance in small- and middle-sized birds, but theoretically it must be of significance in at least the largest flying birds. The difficulty in Currey and Alexander's (1985) study is that only one really large species (a bustard, *Ardeotis kori* Burchell 1822; 16.3 kg) is included. I do not think that it is just a matter of chance that the femur of that species has the relatively thinnest wall of all 220 bones from the 55 Recent species sampled in their study (the relative thickness of the wall of that bone is 6.5 percent of the outer diameter of the bone, or inner diameter/outer diameter = 0.87). This femur is shown in Fig. 14 as "bustard." Humeri from two additional large birds (a swan, *Cygnus olor* (Gmelin 1789), and a pelican, *Pelecanus onocrotalus* Linnaeus 1758; see Fig. 14) that I sectioned and measured show that in very large flying birds, the wall of the bony tube can be even thinner (about 5.0 percent of the outer diameter). Finally, measurements from the long bones of the huge pteranodontid pterosaurs have a relative thickness of the humeral wall of about 4.2 percent, which is the closest known value to the theoretical optimum of 3.5 percent (Bramwell and Whitfield, 1974; Currey and Alexander, 1985; Bühler, 1986). Taken together, these facts suggest that in very large flying birds the walls of the long bones are relatively thinner than in smaller birds and that the problem has to be restudied.

A major consideration that has not been included in these analyses of the relative thicknesses of the walls of tubular long bones is the relationship between the outer diameter of these bones and body size. The strength of these tubular bones depends on several factors, one of which is the thickness of the wall and another is the outer diameter of the bone; the second may be the more important. Hence, large birds may have larger

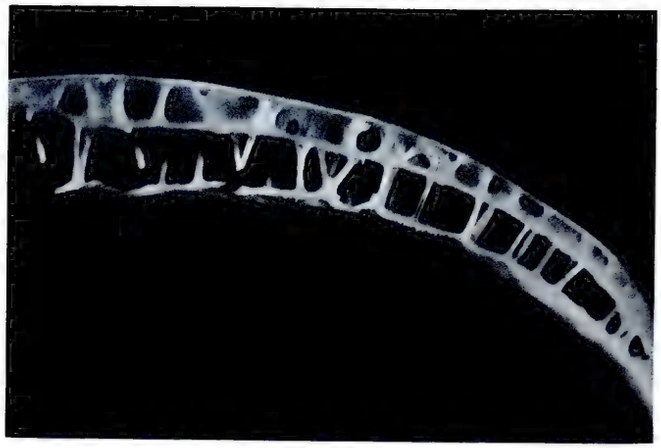

Figure 5. Two-story construction of a corvid braincase (*Pica pica*).

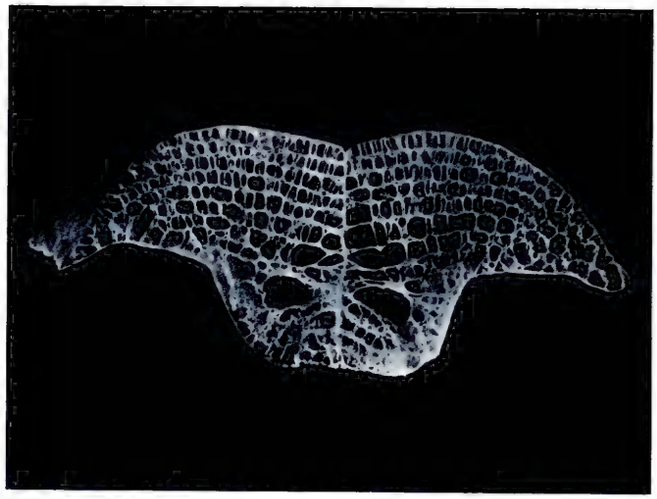

Figure 7. Multistory structure in the skull wall of the brow region of a Tawny Owl (*Strix aluco*). Width of bone is 3 cm.

diameter bones relative to body size that would be stronger in spite of their walls being relatively thinner to the diameter of the bone. A third important factor is the relative slenderness of the bone: A long and thin bone that is pressed along its longitudinal axis can bend sideways and finally break more easily than a short bone of the same cross-section. Thus, the analysis is more complex than that reported in the literature.

In diving birds, the correlation between bone wall thickness and body size is clearer. A relatively high body density is advantageous for divers, and avian divers have relatively thick-walled bones, functionally comparable to the lead weights used by human divers. The humerus of the loon, *Gavia immer* (Brünnich 1764), for example, has a relative thickness of 21.3 percent. The thicker wall in such cases does not mean automatically that these bones are adapted to larger bending stresses.

SANDWICH CONSTRUCTION

A visually impressive weight-reducing strategy is the bony "sandwich" construction best seen in the walls of the avian braincase, but also found in the palate, in the plates of the sternum, and in the ends of long bones. Sandwich bone consists of a thin inner and outer layer of bone separated by a large number of minute bony columns perpendicular to the peripheral layers or by an irregular spongiosa of bony spicules. Corrugated cardboard is an example of sandwich construction. Sandwich construction can be one sandwich layer thick, two-layered as in some corvids (Fig. 5) or multilayered as in some strigids (Figs. 6–9). Such systems can result in extreme weight reductions in structural bone (Bühler, 1970). A 5-cm-long and 3-cm-wide skull of the Red-necked Nightjar, *Caprimulgus ruficollis* Temminck 1820, for example, weighs less than 0.5 g (Figs. 10, 11).

Extant birds have evolved a variety of sandwich bony structures, especially in the braincase (Bühler, 1972, 1986). The ontogenetic development of sandwich bone in the braincase can be readily observed macroscopically in passerine birds with the appearance of a punctuated appearance of the bony surface known as "pneumatization" replacing a clear, uniform surface. This modification can be used to age most passerine birds up to almost 1 year of age (Winkler, 1979; Warncke and Stork, 1985).

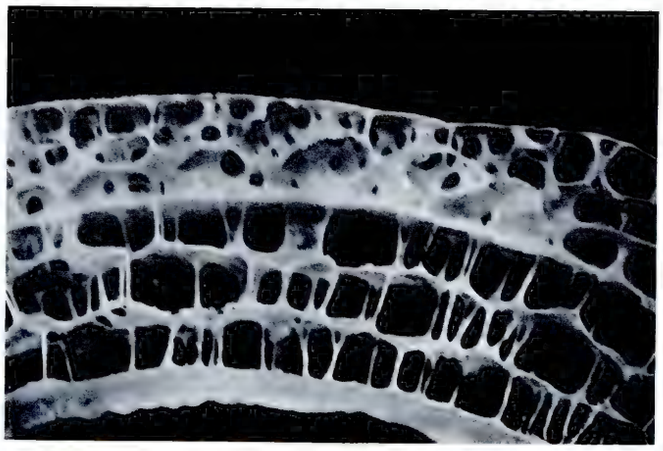

Figure 6. Four-story construction of the braincase of a Long-eared Owl (*Asio otus*).

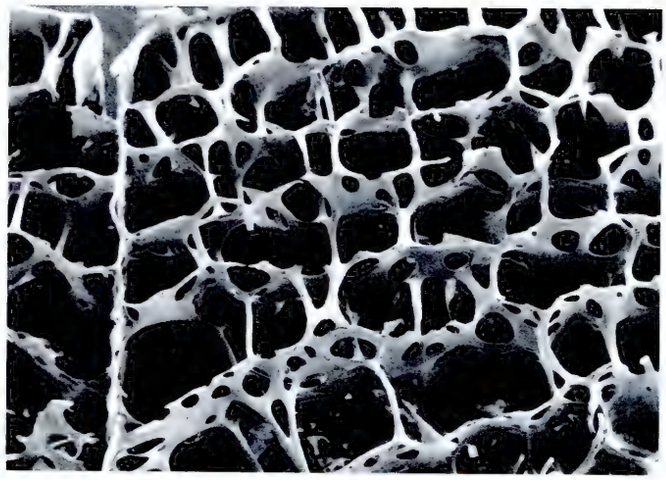

Figure 8. Enlargement of scanning electron microscope photograph of a cross-section of the braincase wall of *Strix aluco*. Width of bone included in image is 6 mm.

Figure 9. Scanning electron microscope photograph of a forked bony beam from the interior of the braincase wall of *Strix aluco*. Section included in image is 1 mm wide.

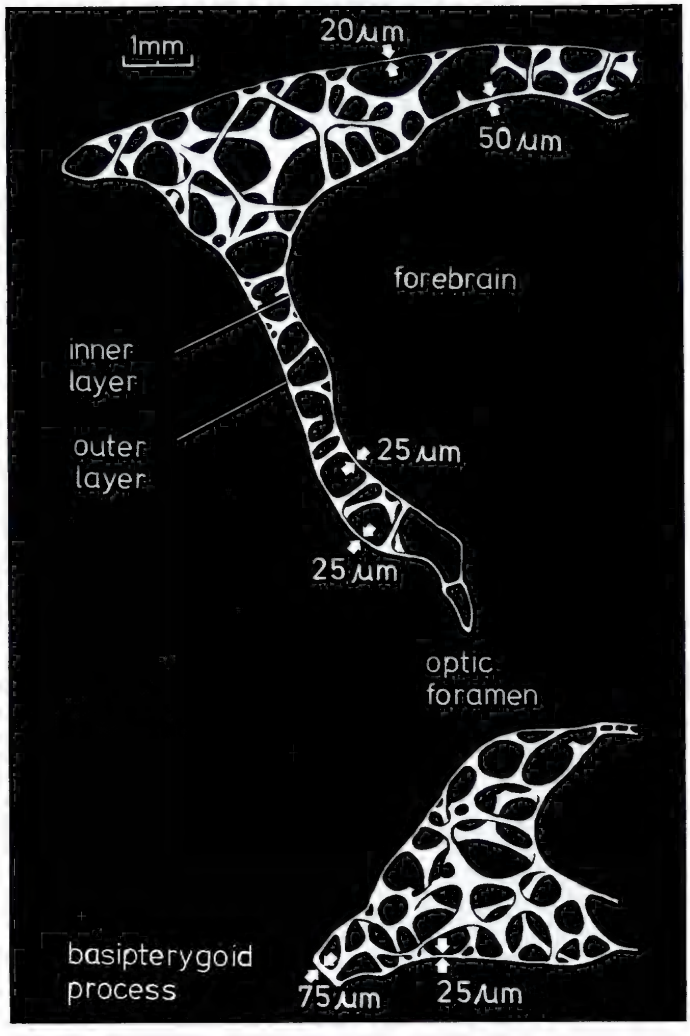

Figure 10. Cross-section through the skull capsule of a Red-necked Nightjar (*Caprimulgus ruficollis*). Extreme weight reduction is achieved by formation of very loose cancellous tissue and very thin cover lamellae. Surprisingly, the exterior lamellae are the thinnest, less than 1/50 mm in some areas of the parietal region. The exterior lamella is thickest in the arthrodia surface of the basipterygoid process (on which the movable palate skeleton slides).

PNEUMATIZATION

Probably the best-known weight-reducing strategy in birds is the substitution of air for marrow or marrow-like tissue in the cavity of hollow bones. This substitution can occur in the cavities of long bones, within sandwich bony plates, within voluminous bones such as vertebrae, and in the skull and jaws. Pneumatization as a process begins either from the nasal cavities, from the middle ear cavities, or in the postcranial skeleton from the air sacs of the lung system (Winkler, 1985). All air-filled bones have a connection to the atmospheric air; hence, the pneumatized bones can be detected by openings (pneumatic pores, foramina, or fossae; e.g., Fig. 1, detail 2) in their walls. It must be noted that extreme care must be taken to distinguish pneumatic openings in bones from other foramina, e.g., for blood vessels, passing into the internal cavity of the bones; no simple set of characteristics distinguish pneumatic openings from other openings in bones. It must be stressed that pneumatized bones are mechanically advantageous in withstanding large bending moments because of the placement of the bony material far from the center of bending, not because they are filled with air. The advantage of the typical lightweight, hollow avian bone thus stems from two different factors, namely (1) being large diameter, thin-walled tubular construction and (2) possessing an air-filled sac in the internal cavity instead of marrow, i.e., less tissue within the body.

Air-filled lightweight bones can possess additional biological functions. For example, in owls the broadening of the braincase made possible by air-filled sandwich bone, and thus the enlargement of the distance between the ear openings, is a basic condition for acoustical localization used by these predators to locate their prey (Bühler, 1972, 1989). In nightjars (Caprimulgidae), the broadened skull base is a basic condition for the spreading mechanism of the lower jaw (Bühler, 1970). In passerine finches, the pneumatized skull roof helps to keep the brain warm (Warncke, 1987).

BOUNDING LAYERS OF COLLAGENOUS FIBERS

Portions of pneumatized sandwich bone, especially the inner and outer layers of bone and the individual interconnecting bony

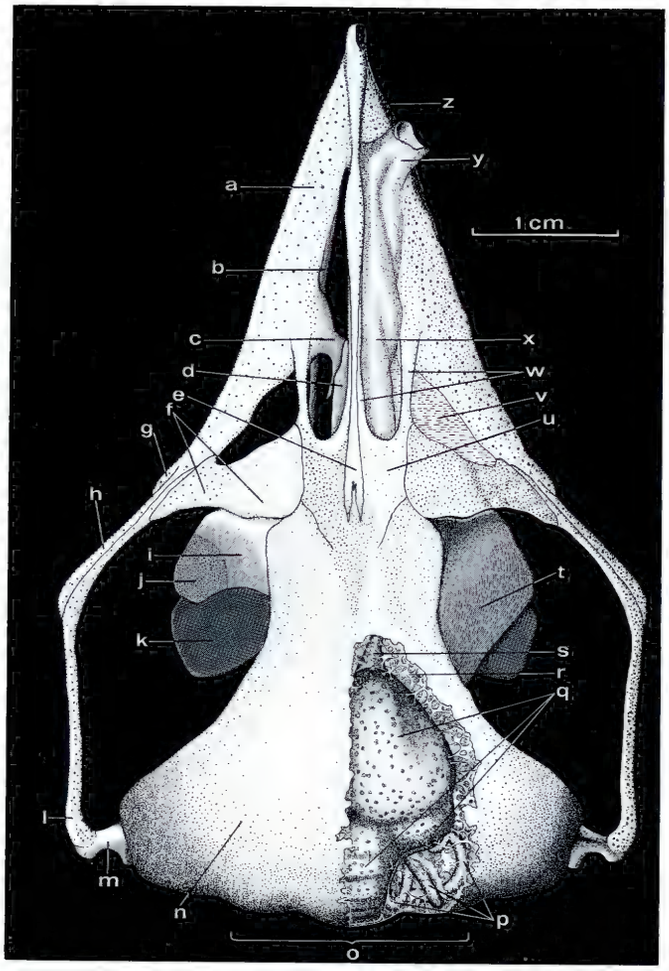

Figure 11. Skull of a Red-necked Nightjar (*Caprimulgus ruficollis*), in dorsal view. The exterior lamella (**n**) of the sandwich shell was removed in the right region of the skull capsule. In terms of form, the inner bony lamella (**p, q, s**) is deceptively close to the interior auditory apparatus, the brain, and the olfactory nerve that it encases. The bony beams (**r**) brace and guy the external and internal bony lamellae against one another (cf. Fig. 10). The brain capsule is approximately twice as wide as the area (**o**) that the brain and inner ear organs occupy. Abbreviations: **a,** premaxilla–maxilla complex; **b,** premaxilla process of the palatine; **c,** palatal process of the maxilla; **d,** vomer; **e,** frontal process of the premaxilla; **f,** prefrontal; **g,** alveolar process of the maxilla; **h,** jugal process of the maxilla; **i,** ectethmoid; **j,** unossified tip of the ectethmoid; **k,** palatine; **l,** jugal–quadratojugal complex; **m,** quadrate; **n,** outer bony lamella of the wall of the braincase; **o,** width of the brain; **p,** bony tubes of the semicircular canals of the internal ear; **q,** inner bony lamella of the wall of the braincase; **r,** bony beams between the inner and the outer lamellae; **s,** bony tube around the olfactory nerve; **t,** subocular hammock-like membrane; **u,** nasal; **v,** membrane of the antorbital foramen (vacuity); **w,** premaxillar and maxillar processes of the nasal; **x,** cartilaginous nasal capsule; **y,** cartilaginous tube of the nostril; **z,** horny sheath of the upper beak.

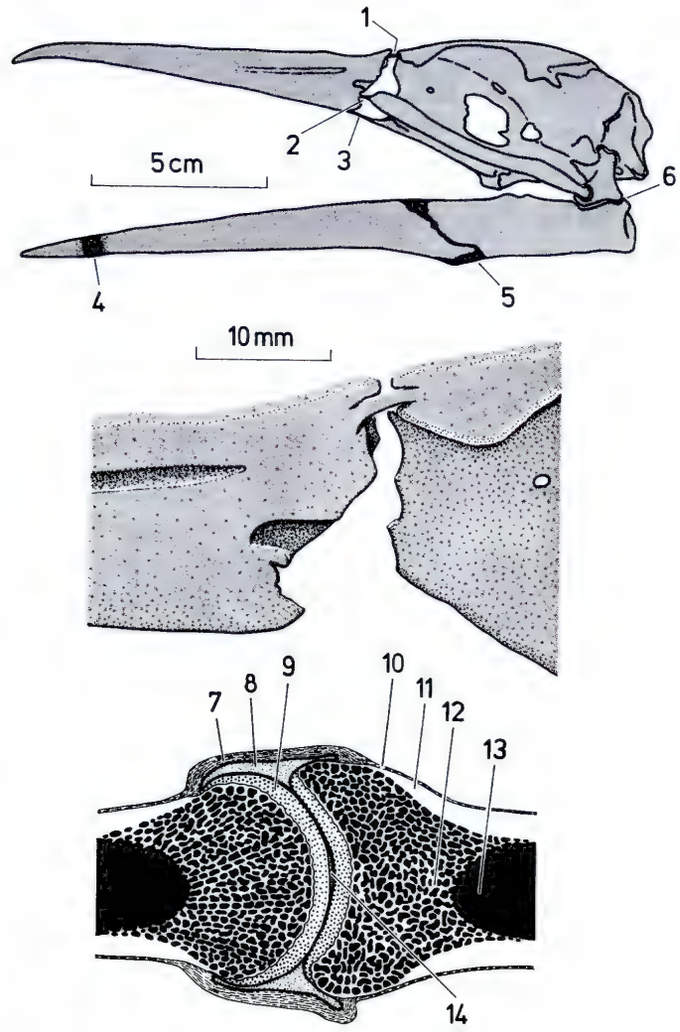

Figure 12. Above: skull of a gannet (*Sula bassana*) with plate-spring articulations (**1–5**); "normal" articular joint (**6**) between mandible and quadrate. Center: the main hinge of the upper jaw of the gannet, enlarged to demonstrate the low material need compared with that of a real diarthrodial joint, bottom (diagrammatic). **7,** Joint capsule; **8,** synovial fluid; **9,** joint cartilage; **10,** periosteum; **11,** compact bone; **12,** spongiosa; **13,** marrow; **14,** joint cleft.

struts, are often surprisingly thin. The inner bony layer of the sandwich bone of the braincase wall of *Caprimulgus ruficollis* mentioned earlier is, for example, only 20 μm thick, i.e., one-fiftieth of a millimeter (Fig. 10). This thin sheet of bone is covered and strengthened by an outer layer of collagenous fibers (the periosteum) and a second layer of collagenous fibers (the lining air sac), thus forming a special microsandwich within the main bony sandwich (Bühler, 1970). The strength of the bounding layers of collagenous fibers against tensile forces prevents the thin bony sheet from buckling because of compressive stresses resulting from external and muscular forces acting on the sandwich bone.

PLATE-SPRING ARTICULATIONS

Wherever individual bones come together, some specialized type of contact structure develops; this contact structure varies from a suture to some type of movable articulation. Many birds have additionally developed an unusual type of bony articulation, a kind of synostosis, within the rami of the lower jaw, within the upper jaw, within the palatal bridges, and/or between the upper jaw and the braincase. These synostoses are bending zones with-

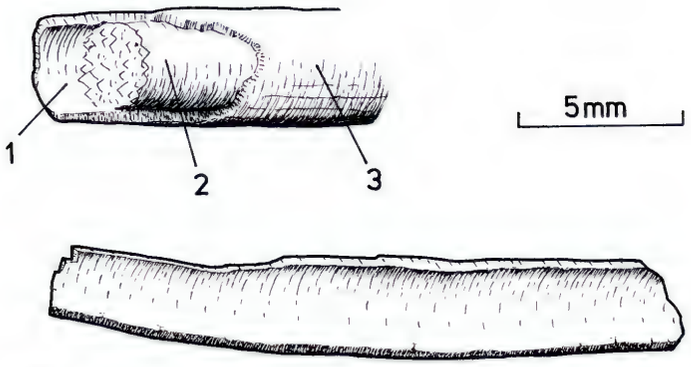

Figure 13. Two enlarged details of the fossilized long bones of the London *Archaeopteryx* specimen. Above: part of an ulna (**1,** inner wall of the bone; **2,** crystalline calcite filling the cavity of the bone; **3,** complete tubular part); below: the bony wall of the tubular part of a femur.

in a bony structural element (flexion zone, plate-spring articulation) and are of particular importance for both the kinematics of the upper jaw and the lateral spreading movements of the lower jaw (Bühler, 1981, 1986). Of the amount of material needed in a diarthrosis and in a synostosis of comparable size, it is obvious that these bony articulations are material-saving structures (Figs. 2, 12).

MISCONCEPTIONS

Various aspects of the avian lightweight skeleton are so well known that some misconceptions have become widespread in the literature. The most important misconception is that birds are unique in possessing hollow bone; this configuration is that most typical for tetrapod long bones. Another misconception is that hollow bones are stronger than solid bones. Hollow bones are actually weaker than solid, but they are lighter in weight (Bock, 1974).

In many textbooks, one can find statements that some avian groups such as the gulls (Laridae), the rails (Rallidae), the flightless parrots of New Zealand, *Strigops habroptilus* Gray 1845, and the kiwis (Apterygidae) do not have hollow bones, an assertion that is wrong in two ways. First, these birds do have hollow bones, even if the internal cavity of these bones is filled with marrow. Second, parts of at least their skull bones are pneumatized, although these regions are more restricted than in most other birds. In *Strigops,* even parts of the postcranial skeleton are pneumatized.

Also, the common statement that avian bones are generally pneumatized is wrong because in most birds the distal limb bones, the femur, the jugal bar, the first two cervical vertebrae, and the caudal vertebrae are filled with marrow. Furthermore, the statement that all avian bones are hollow is not correct. In some birds, the jugal bar is solid, and shortly before the time of egg-laying the hollow limb bones of female birds, which are normally filled with marrow, are filled more or less with an unusual "medullar bone" that functions as a calcium deposit for the mineral salts required for forming eggshells. Because this transformation from normal marrow to medullar bone occurs only a few days or weeks before egg laying, the existence of medullar bone in fossil avian bones can be an important indicator of female individuals, of breeding activities, and even of paleoclimatic conditions (e.g., Ballmann, 1979).

Finally, I wish to discuss a statement by Prange et al. (1979:

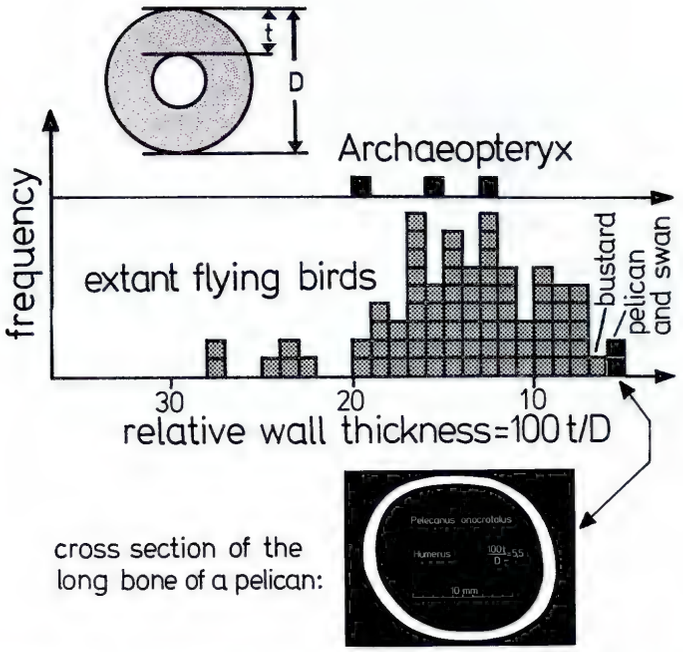

Figure 14. Frequency distribution of the relative wall thickness of the long bones of a random sample of extant flying birds (80 bones of 23 species) compared with three measurements of *Archaeopteryx.* One square = one bone; data of the stippled squares from Currey and Alexander (1985). Note that the three most thin-walled bones are from the three largest species of the total sample (bustard, pelican, and swan).

105): "Contrary to the common expectations, the skeletons of birds are not lighter than those of mammals." This conclusion was deduced from the fact (shown by the authors) that the allometry of skeletal mass to body mass in birds is very similar to that in mammals. The question is whether or not this deduction is admissable. As a general principle, light and heavy refer to the relation between weight and volume, so in this sense the statement is wrong. But in a wider sense, one could accept the relation between weight and mechanical efficiency. Then the question arises of whether or not the mechanical loading of the skeleton of living animals is a simple function of the body mass. At least between birds and mammals, which move in such different ways, this is unlikely. Furthermore, at the same time that

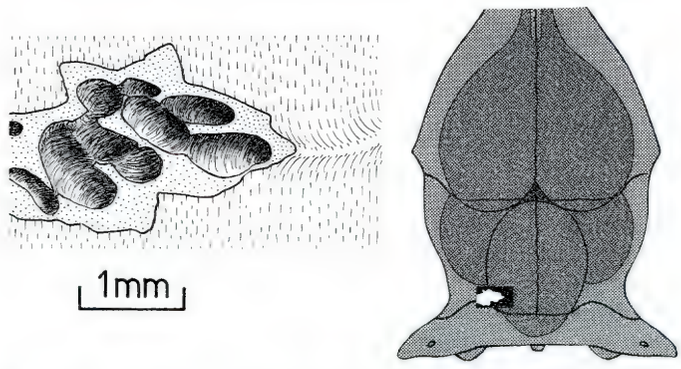

Figure 15. Earliest pneumatized structure of a bird. Right: braincase of the London *Archaeopteryx* (diagrammatic) showing the side from which is drawn the enlarged detail (left).

selection pressure diminishes the weight of a skeleton, it probably also diminishes, to a certain degree, the weight of the soft parts of the body. So the constant skeleton mass to body mass relation does not indicate that the avian skeleton in general is as heavy as the mammalian skeleton.

THE EARLY EVOLUTION OF LIGHTWEIGHT STRUCTURES

To determine at what time in the geologic past some of these lightweight adaptations in the avian skeleton might have originated, I studied the braincase and long bones of *Archaeopteryx* (London specimen) and the skulls, vertebrae, and the relative thickness of the walls of the long bones in different theropod dinosaurs. Even though the London specimen of *Archaeopteryx* was described in detail by Sir Gavin de Beer (1954), it is still possible to discover interesting new facts such as the following: (1) The long bones appear solid because they are filled with mineral matter, and de Beer (1954:30) stated that "it is impossible to conclude that this matter has not replaced bone or that the bone was hollow." (I should note that in this section de Beer is considering the evidence of whether or not the skeleton of *Archaeopteryx* was pneumatic, and only indirectly whether or not the bones were hollow.) With a stereomicroscope, one can see very clearly that in all cases in which the long bones have been broken open (i.e., both femora, both tibiae, one ulna, one radius, and one metatarsus), an inner cavity exists in the bone and is filled with lucid and crystalline calcite surrounded by an opaque wall with a smooth inner surface against the crystalline core. The opaque wall is obviously fossilized bone, and the crystalline calcite has been deposited in the central region of the long bones post-mortem. Thus, the London specimen of *Archaeopteryx* has hollow long bones (Fig. 13). This resolves the contradictions between de Beer's description of the London specimen and those of the Maxberg and the Eichstätt specimens (Heller, 1959; Wellnhofer, 1974). (2) The walls of the long bones are relatively thin, actually within the range of variation of the walls of tubular bones in Recent birds (Fig. 14). (3) The London specimen has pneumatized "sandwich" bony structures in parts of the wall of the braincase. This shows that some typically avian lightweight features existed in primitive toothed birds (Fig. 15). (4) The question as to whether or not the hollow long bones of *Archaeopteryx* were pneumatized is still open despite de Beer's (1954:29–31) conclusion.

The study of different theropod bones showed that thin-walled long bones, pneumatized skull bones, and pneumatized postcranial bones (vertebrae) had already evolved in pre-avian archosaurs and that these features were probably inherited by the earliest birds from their non-flying ancestors. This conclusion should not be interpreted as support that birds descended from the theropods, because these lightweight features probably have evolved in several different groups of fossil reptiles.

SUMMARY

This paper describes the different strategies that have been developed within birds to reduce the weight of the body by transforming details of the skeletal system. In addition to the well-known pneumatizations and thin-walled long bones, flat bony bars, fusion of individual bones, sandwich structures in the braincase, loss of teeth, special microsandwiches (of two layers of connective tissue with a bony lammella between), and bony plate-spring articulations help reduce the total weight. Furthermore, misconceptions concerning the avian skeleton are discussed. *Archaeopteryx* and some theropods were studied to develop ideas about the origin of avian lightweight features.

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THE RELATIONSHIP OF HINDLIMB BONE DIMENSIONS TO BODY WEIGHT IN BIRDS

Kenneth E. Campbell, Jr. and
Leslie Marcus

ABSTRACT. An analysis of femur and tibiotarsus least shaft circumference plotted against live body weight in a data set of 795 individuals in 25 orders, 89 families, and 387 species of birds reveals a high correlation between the leg bone dimensions and body weight. No scaling model fits the whole data set very well, but there is a significant fit by different scaling models for some functional and taxonomic groups.

The high correlation observed between leg bone circumference and body weight is related to the support role of the femur and tibiotarsus in birds. A working model to explain this relationship is based on the correct placement of a bird's center of gravity. A cantilever style of support by the femur, as opposed to a pillar style of support, and various aspects of hindlimb locomotory and feeding functions are discussed in an evaluation of the importance of scaling relationships in birds.

The weights of several large, extinct birds are estimated by using the observed relationship of bird bone circumference and body weight in living birds. Estimation of bipedal dinosaur weights requires more careful evaluation of postulated models of dinosaur stance.

Key words: birds, scaling, allometry, geometric similarity, elastic similarity, general structural relation, reduced major axis, body weight, hindlimb function, functional morphology.

INTRODUCTION

In recent years, there have been several attempts to evaluate the relationship between limb bone dimensions and body mass in vertebrates. Prominent among works pertaining to birds are those of Alexander et al. (1979), Maloiy et al. (1979), and Alexander (1983a, 1983b). Important works that pertain to mammals include those of McMahon (1973, 1975a, 1975b), Scott (1985), and Bou et al. (1987). Extrapolating from Recent data, others have attempted to predict body mass of dinosaurs (Anderson et al., 1985), fossil birds (Campbell and Tonni, 1983), and artiodactyls (Scott, 1983).

A principal function of the vertebrate skeleton is to provide support to the body mass. Therefore, it would appear logical that within a series of similarly shaped animals of many different sizes one might expect to find a clear functional relationship between body mass and the size of the supporting skeletal structure. Such a relationship is best termed scaling, "... the study of the influence of body size on form and function" (LaBarbera, 1989:97). Several scaling models have been proposed, each based on differing mechanical considerations of support mechanisms. The books by Schmidt-Nielsen (1984) and McMahon and Bonner (1983) give excellent, readable discussions of scaling.

In addition to support, the relationship between body mass and the size of supporting skeletal structure in vertebrates is related to the fact that the skeleton fulfills a crucial role in locomotion and a separate, sometimes correlated, role in feeding. Because adaptive specialization in birds has led to a considerable diversity of skeletal structures, sometimes within closely related taxa, one problem in developing scaling models is the separation of the skeleton's support role from its locomotory and feeding roles.

One important study of the influence of locomotory or feeding functions on leg bone allometry is that of Scott (1985). Scott discusses the role of adaptive factors in determining limb dimensions and deviations from expected scaling relationships. Variability beyond that predicted by scaling models for distal long bone lengths was cited as one prime example of the role of adaptive factors. Maloiy et al. (1979) recognized that the lengths of hindlimb bones in birds did not scale as expected. Alexander (1983a) showed that in moas and other birds there is a higher correlation between body mass and femur length and diameter than between body mass and tibiotarsus or tarsometatarsus length and diameter, a result comparable to that observed by Scott (1985) for the Bovidae. Alexander (1983a) associated this disagreement with taxonomic differences and not with functional adaptations.

This paper is an outgrowth of a paper by Campbell and Tonni (1983). These authors attempted to estimate the weight of the world's largest known flying bird, the late Miocene *Argentavis magnificens* Campbell and Tonni 1980 from Argentina, by using the relationship between tibiotarsus least shaft circumference and live body weight in 324 individual birds from 19 orders and 45 families. We expanded their data base to test their results using a larger data set and to determine if there were different trends within subgroups of birds. The augmented data set contained 795 individual birds from 25 orders, 89 families, and 387 species.

We review avian hindlimb functional morphology in an attempt to identify the origin of the observed relationship between body weight and hindlimb dimensions. We use the expanded data set to revise Campbell and Tonni's (1983) weight prediction for *Argentavis magnificens* and to estimate the weights of several other extinct birds. We then discuss the applicability of the bird data for estimating the weight of bipedal dinosaurs.

MATERIALS AND METHODS

MEASUREMENTS

The plane of greatest shaft weakness in any long bone is the transverse plane of least shaft circumference, especially when bending moments are the largest stresses bearing upon the bone. The tests of Clark and Alexander (1975) on the breaking strength of quail leg bones, while not quantifiable, provide qualified support for this hypothesis. Biewener (1982) states that stresses resulting from bending moments are likely to be greatest at the midshaft of a bone. Although this may be true, it does not necessarily follow that the midshaft is the weakest part of the shaft. This is particularly true for the tibiotarsus, where fusion of the fibula to the tibiotarsus in the midshaft region often greatly affects shaft geometry.

We used least shaft circumference of the femur and tibiotarsus instead of least shaft diameter as our key measure for analysis because in cross-section the shafts of both femora and tibiotarsi are not perfectly round tubes. However, we did not determine to what extent deviation from a round tube contributed to the error value.

We measured the circumference by wrapping a narrow strip of cellophane tape around the shaft of the bone in the plane of its least circumference. This plane was determined, if possible, by first finding the least width and least depth of the shaft, although in some cases a qualitative determination was required if the least width and least depth did not coincide. The tape was marked in the area where the two ends overlapped, laid out flat, and the distance between the lines measured with calipers. Several researchers assisted us in taking these measurements, so it is not possible to state the quality of the calipers or the exact degree of accuracy present in the data. We calculated the circumference from width and depth for the smallest specimens because their circumferences were extremely difficult to measure directly.

This procedure differs from the work of Alexander (1983b), Alexander et al. (1979), and Maloiy et al. (1979), in which the measure used was the sagittal diameter measured midway between the proximal and distal ends. Our data also differ from those of Prange et al. (1979) because they measured width at the midpoint of the shaft across a diameter parallel with the anteroposterior axis of the animal, and from those of Anderson et al. (1985) because they used midshaft circumference, which does not always coincide with the least shaft circumference.

The least shaft circumference of a bird femur usually lies near or distal to the midpoint of the shaft length. Exceptions to this are noted in larger birds, especially the ratites, in which the least shaft circumference lies proximal to the midpoint of the shaft. The position of the least shaft circumference of bird tibiotarsi varied among the many species of birds we measured, but it was almost always at or distal to the midpoint of the shaft length. In the great majority of specimens measured, it occurred in the distal one-third of the shaft length.

In addition to measurement error associated with each individual researcher, there were other sources of potential error in the data. There is no control over the time of day, season, or year when any given specimen was collected, and each time factor has a potentially large impact on the registered weight of the bird. Any sick, and thus probably underweight, specimens, could not be identified. Effects of migratory habits on weight were ignored. The data came from many collections and the specimens were taken in the field by numerous different collectors and weighed on different types of scales at differing periods of time after being taken. Only adult birds, as determined by the degree of ossification of the leg bones, were used in this study.

BIVARIATE RELATIONSHIPS

Bivariate plots and regressions of logarithm to the base 10 of weight, i.e., $\log_{10}$(weight), on $\log_{10}$(femur circumference) and $\log_{10}$(tibiotarsus circumference), and the latter two on each other, provide the most important display of our results for comparing groups of birds. One can visually assess the strength of the correlation and the linearity of the data.

We predicted the weights of fossil birds using the standard regression fit of log(weight) on log(circumference) (Model I of Sokal and Rohlf, 1981). LaBarbera (1989) reviewed scaling models in general and Rayner (1985) presented a clear, comprehensive discussion of fitting such models in birds when the data include measurement error and taxonomic diversity. We were unable to control or determine measurement error, but the hierarchical nature of our data corresponds to the interspecific situation described in Rayner (1985: fig. 1b). In that case, one is interested in finding the functional relation between two measures in a higher level (e.g., family or order, or other grouping) and has data for many species within the higher taxa and samples of varying numbers of individuals for the species.

A general structural relation (*gsr*) is the least restrictive regression model, and Rayner (1985) gave the procedure for fitting the *gsr*. He clearly stated how the assumptions implied in other fitting schemes are all special cases of the *gsr*.

If at all possible, one should fit the *gsr* to the species means, adjusting for the within species variation and covariation. If assumptions about the nature of the variability and covariability within species cannot be made with confidence, then the reduced major axis (*rma*) is the most appropriate model. Details are given in Rayner (1985). Because sample sizes were small within each species and morphofunctional group, we pooled the within species variability and covariability over all species and used these statistics to estimate the general structural relation (*gsr*). Ordinary least squares regression (OLS), or prediction regression, used here for estimating body weights, and the major axis (*ma*) are also special cases of the *gsr*.

If the within and among species standard deviations are equal, the *gsr* simplifies to the *rma*. This is estimated as the ratio of the standard deviations of the two variables among species. It is given the sign of the correlation coefficient. The *rma* ratio for the pooled data within species tended to be similar to that among species, but the standard error was so high for the ratio within species as to be uncertain. Where possible, both the *gsr* and *rma* were calculated. Rayner (1985:425) points out that "If the error distribution [variability within species in our case] is unknown, the r.m.a. models exhibit both within- and between-population variation with the least bias." He goes on to suggest that the *gsr* is best, but if the subpopulation variability is not available then the *rma* should be used. An empirical study of McArdle (1988) gives additional support to the use of the *rma*.

We report the *gsr*, *rma*, and *ma* slopes together with their 95 percent confidence intervals for each group. A nested analysis of variance (ANOVA) of the log data was used to generate sums of squares and cross-products for groups, families, genera, species, and individuals within species using PROC NESTED in PC SAS (6.03). Correlations, least-squares regressions, *rma*, *ma*, the covariance ratio estimate (Kuhry and Marcus, 1977), and both the correlated and uncorrelated form of the *gsr* were estimated from the results of the ANOVA using a program written in Quick Basic. For the results reported here, we used species means

weighted by the number of specimens available for each species. This was thought to reflect the variability in the data best, and it is a natural consequence of using the nested ANOVA.

Confidence intervals for the slope of the *rma* and *ma* were computed following the exact method of Jolicoeur (1990), as he has shown that some of Rayner's (1985) earlier formulae for the *rma* give unreasonably large confidence intervals. Jolicoeur favors the *ma* (which makes the assumption that the ratio of error variances is 1) to the *rma* because of better behavior of the slope confidence intervals. However, our correlations are high and samples large enough for these effects to be minimal. Furthermore, the *ma* is sensitive to weight and linear dimension relationships in log form. A suitable transformation, such as the cube root of weight, removes some of this difficulty (Jolicoeur, 1990). This was not attempted here because we wished to keep the data in a form most comparable to scaling model parameters and to be consistent with the earlier work of Campbell and Tonni (1983).

Three scaling models were tested by seeing if the 95 percent confidence intervals contained the parameter for the model. The models were elastic similarity, compressive similarity, and geometric similarity, or isometry. Isometry predicts that the coefficient of log(circumference) or slope will be 3 in the log form of the allometric formula because identically shaped birds will increase weight to the third power of their linear dimensions according to this model. Compressive similarity predicts a coefficient of 2 because failure under compression leads to a prediction that cross-sectional area, which is approximately proportional to the square of the diameter (or circumference), will keep pace with weight. McMahon (1973) has shown that bending force failure scales as the 8/3 power of diameter (or circumference = π•diameter for an assumed circular bone) and bones that follow this model are said to scale according to elastic similarity. Therefore, we may see which of these scaling models fits our data best. Because our data are heterogeneous and we have no information about bone thickness and have not considered cross-sectional shape, if a model provides a good fit it only indicates that the law may be appropriate and that the problem should be studied in greater detail.

We analyzed the overall data set (AL) and the following taxonomically and morphologically determined groups of the data. The families included in each group are listed in Table 1 and in their respective plots.

AN: order Anseriformes; a taxonomic group with low diversity in morphology but a high size diversity.

CH: order Charadriiformes; a taxonomic group with high diversity in morphology and size.

HB: heavy-bodied terrestrial birds; unrelated birds that are similar in morphology (relatively short-legged and heavy-bodied) and have a diverse size range.

LL: long-legged birds; unrelated birds of diverse size that share the trait of having relatively long legs.

MF: marine flyers; unrelated marine birds of diverse morphology and habits.

NP: non-passerine birds; all non-passerine families in the data set.

PB: predatory birds; a morphological grouping of predatory flying birds (hawks, falcons, ospreys, and owls).

PS: order Passeriformes; a taxonomic group of all passerine families, with a wide diversity in habits but general similarity in form.

SF: order Apodiformes; a taxonomic group of very small flying birds that do not use their legs for much more than perching.

Table 1. Names of the 89 families that comprise each subgroup of the data set are given here. For explanation of grouping, see text.

AL: All 89 families listed below.

AN: Anatidae and Anhimidae.

CH: Scolopacidae, Recurvirostridae, Rostratulidae, Jacanidae, Haematopodidae, Phalaropodidae, Burhinidae, Charadriidae, Thinocoridae, Laridae, Stercorariidae, Rhynchopidae, and Alcidae.

HB: Tinamidae, Apterygidae, Anhimidae, Cracidae, Numididae, Phasianidae, Tetraonidae, Meleagridae, Turnicidae, Pteroclidae, and Columbidae.

LL: Struthionidae, Rheidae, Phoenicopteridae, Plataleidae, Ardeidae, Cochleariidae, Scopidae, Ciconiidae, Rallidae, Gruidae, Aramidae, Otididae, and Burhinidae.

MF: Diomedeidae, Procellariidae, Hydrobatidae, Phaethontidae, Pelecanidae, and Fregatidae.

NP: Sixty-nine families of non-passerines, in alphabetical order. Accipitridae, Alcedinidae, Alcidae, Anatidae, Anhimidae, Anhingidae, Apodidae, Apterygidae, Aramidae, Ardeidae, Burhinidae, Charadriidae, Ciconiidae, Cochleariidae, Coliidae, Columbidae, Cracidae, Cuculidae, Diomedeidae, Eurypygidae, Falconidae, Fregatidae, Gaviidae, Gruidae, Haematopodidae, Heliornithidae, Hydrobatidae, Jacanidae, Laridae, Meleagridae, Meropidae, Momotidae, Numididae, Nyctibiidae, Opisthocomidae, Otididae, Pandionidae, Pelecanidae, Phaethontidae, Phalacrocoracidae, Phalaropodidae, Phasianidae, Phoenicopteridae, Picidae, Plataleidae, Podicepedidae, Procellariidae, Psittacidae, Pteroclidae, Rallidae, Ramphastidae, Recurvirostridae, Rheidae, Rhynchopidae, Rostratulidae, Scolopacidae, Scopidae, Spheniscidae, Stercorariidae, Strigidae, Struthionidae, Tetraonidae, Thinocoriidae, Tinamidae, Trochilidae, Trogonidae, Turnicidae, Tytonidae, Vulturidae.

PB: Accipitridae, Falconidae, Pandionidae, Strigidae, and Tytonidae.

PS: Dendrocolaptidae, Furnariidae, Formacariidae, Pipridae, Tyrannidae, Hirundinidae, Corvidae, Paridae, Troglodytidae, Mimidae, Turdidae, Sylviidae, Laniidae, Vireonidae, Coerebidae, Icteridae, Thraupidae, Fringillidae, Emberizidae, and Ptilogonatidae.

SF: Trochilidae and Apodidae.

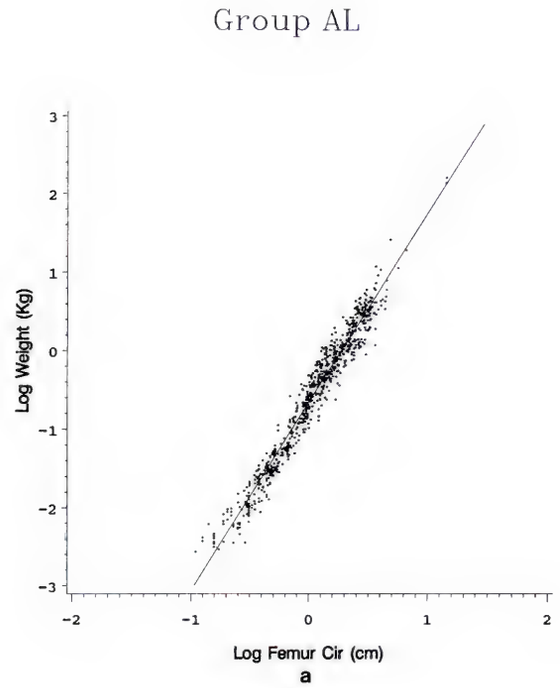
SW: Gaviidae, Podicipiedidae, Spheniscidae, Phalacrocoracidae, Anhingidae, and Phalaropodidae.

SW: swimmers; a morphological group of unrelated swimming birds.

RESULTS

The plots for all of our data and some of our subgroups are given in Figs. 1–7 for the logarithm (base 10) of weight against the logarithm of least circumference of the femur and tibiotarsus. The individual *rma* lines for all subgroups are plotted in Fig. 8. The two groups AN (order Anseriformes) and PB (orders Accipitriformes and Strigiformes), which overlap considerably in weight but have different-sized limb bones, are contrasted in Fig. 9. Figures 1–8 have the same scaled axes so they can be compared over groups. Slopes and intercepts, with 95 percent confidence intervals, are given in Table 2. The confidence intervals are asymmetrical except those for OLS regressions.

The *rma*'s and *ma*'s, as well as the general structural equation fit and their confidence intervals, are presented in Table 2. There is diversity in the slopes of the lines among groups. There is little difference among the *gsr*, *ma*, and *rma* results; therefore, the *rma* results will be discussed in what follows. The estimation equations based on OLS are also given in Table 3 and that for AL is used for weight prediction later in the paper.



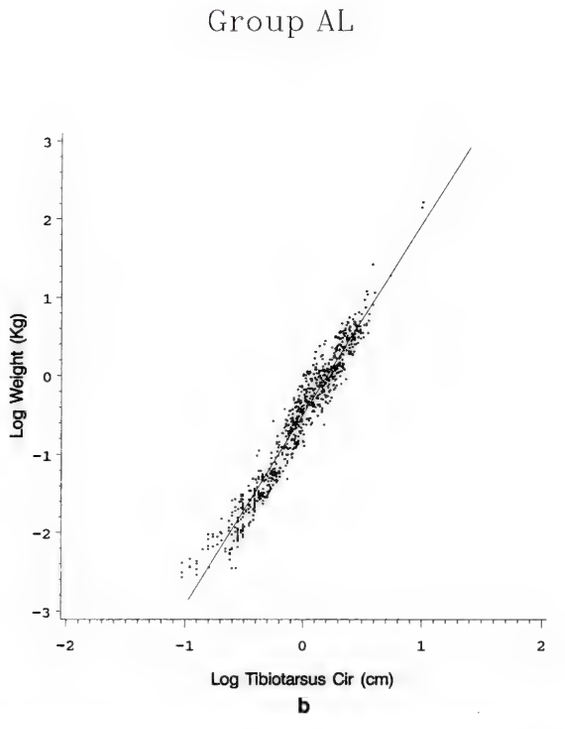
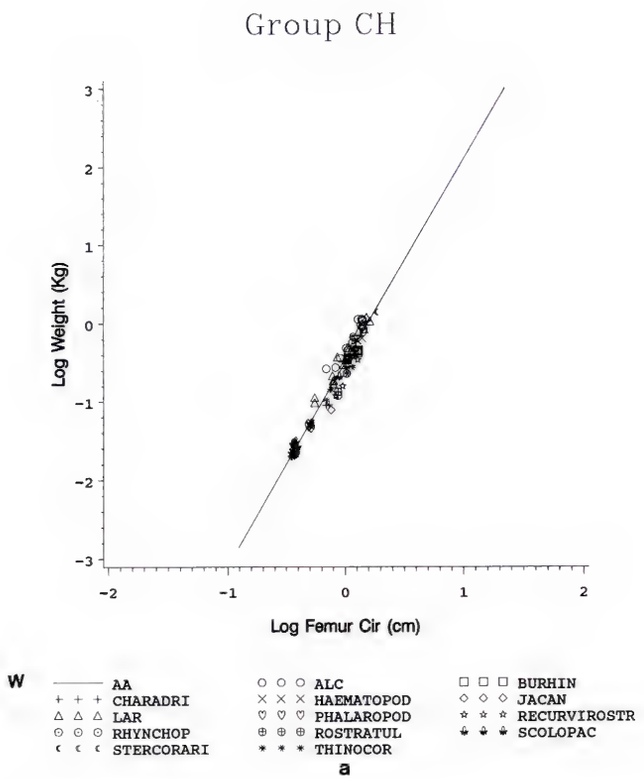


Figure 1. Plots of (**a**) $\log_{10}$(femur circumference) vs. $\log_{10}$(weight) and (**b**) $\log_{10}$(tibiotarsus circumference) vs. $\log_{10}$(weight) for 795 individual birds in 25 orders, 89 families, and 387 species.



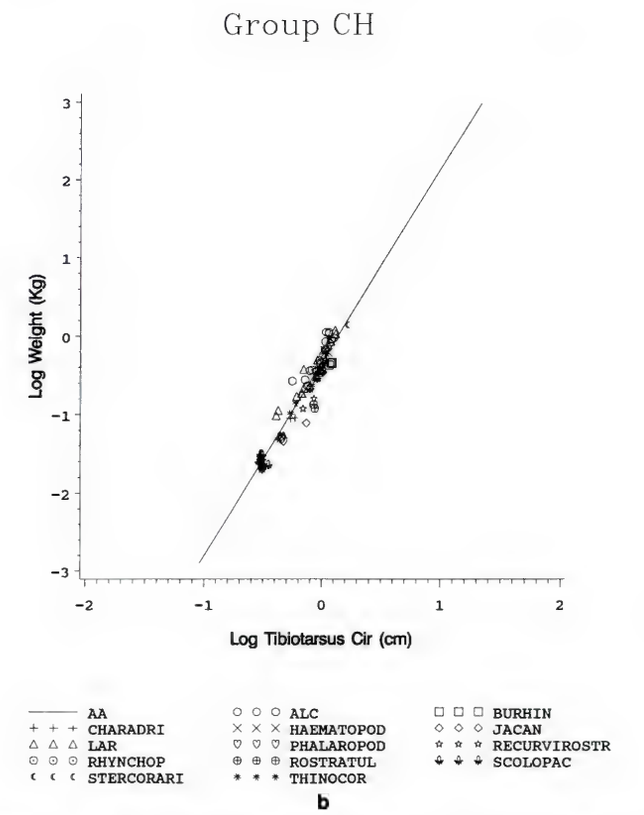
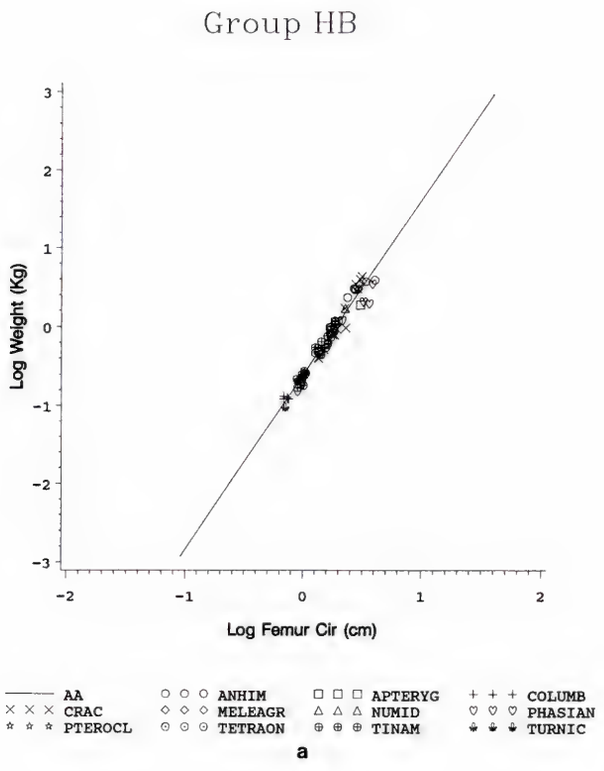
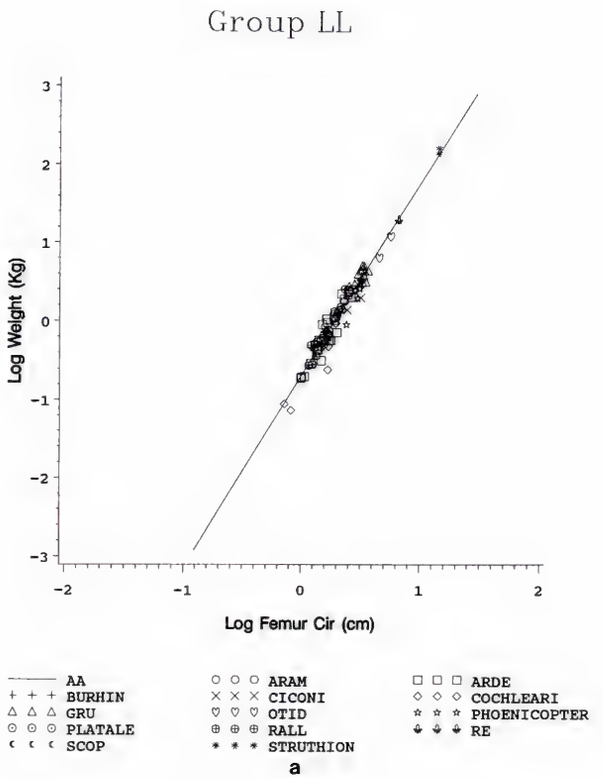
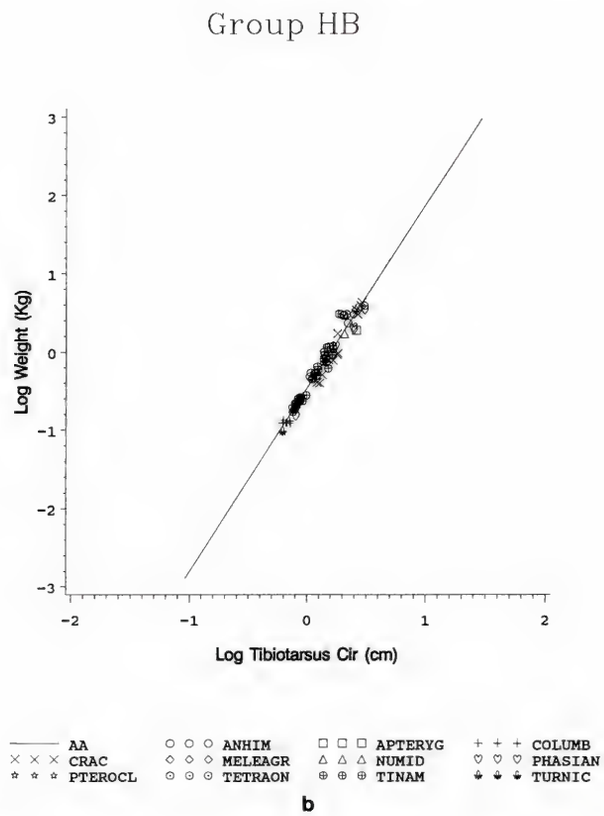


Figure 2. Plots of (**a**) $\log_{10}$(femur circumference) vs. $\log_{10}$(weight) and (**b**) $\log_{10}$(tibiotarsus circumference) vs. $\log_{10}$(weight) for subgroup CH (=order Charadriiformes). Separate symbols for each family. In this figure and Figs. 3–7, family names are given minus ending *-idae*. In this and all other figures where it appears, **AA** = reduced major axis (*rma* in text).

For log weight and log femur circumference regressions, the *rma* slopes vary from 2.071 for the Apodiformes (SF), near the 2.0 predicted by compressive similarity, to 2.673 for the swimming birds (SW), near the value of 8/3 (2.67) predicted by elastic similarity scaling. For the femur, the groups PB, LL, CH, PS, and SW show values consistent with elastic similarity scaling of







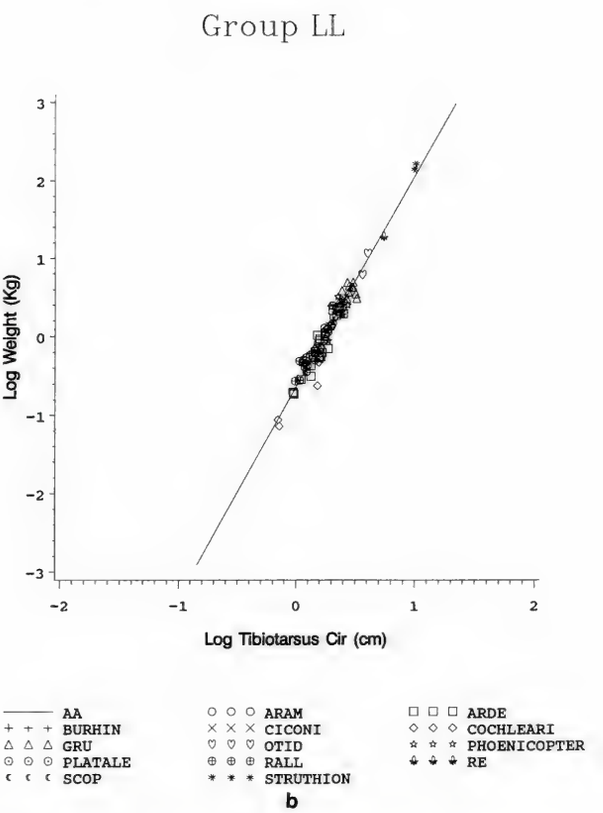


Figure 3. Plots of (**a**) $\log_{10}$(femur circumference) vs. $\log_{10}$(weight) and (**b**) $\log_{10}$(tibiotarsus circumference) vs. $\log_{10}$(weight) for subgroup **HB** (=heavy-bodied terrestrial birds).

Figure 4. Plots of (**a**) $\log_{10}$(femur circumference) vs. $\log_{10}$(weight) and (**b**) $\log_{10}$(tibiotarsus circumference) vs. $\log_{10}$(weight) for subgroup **LL** (=long-legged birds).

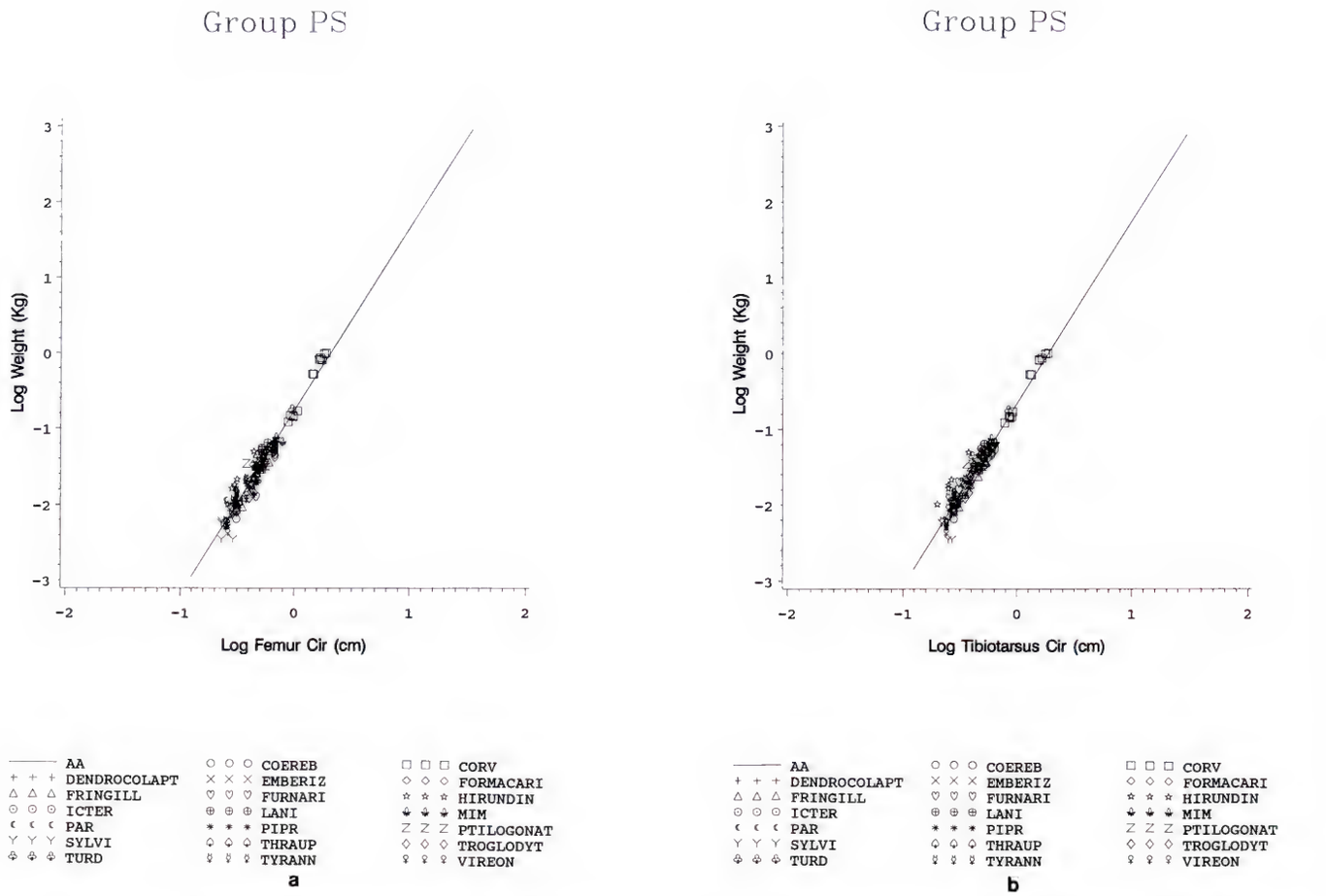


Figure 5. Plots of (**a**) $\log_{10}$(femur circumference) vs. $\log_{10}$(weight) and (**b**) $\log_{10}$(tibiotarsus circumference) vs. $\log_{10}$(weight) for subgroup **PS** (=order Passeriformes).

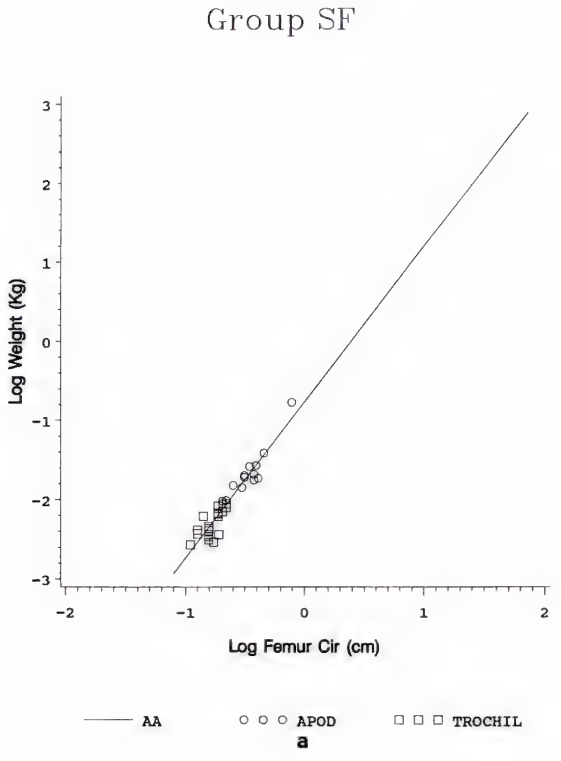
8/3. The groups MF, AN, and SF are consistent with the model of compressive similarity. CH is the only group whose confidence interval comes very close to 3.0, the value for isometry. The heavy-bodied (HB), non-passerines (NP), and all birds together (AL) fit none of the scaling models. Because NP and AL are heterogeneous combinations of the groups that show agreement with one or another of the scaling models, it is possible that the heterogeneous HB group could also be subdivided if more data were available.

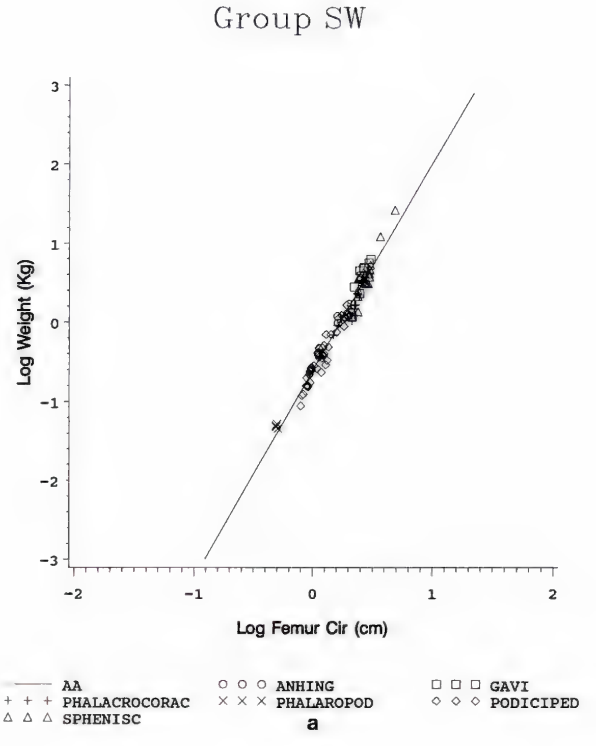
The tibiotarsi follow similar trends, but there is greater diversity among slopes. The lowest value for the tibiotarsus is for the Anseriformes (AN), 1.951, and the largest, 2.758, is for the long-legged group (LL). The same groups as for the femur contain the parameter for elastic similarity; however, among these, PB, LL, and CH also come close to including geometric similarity. SF and AN are still consistent with a coefficient of 2.0, whereas the MF confidence interval also contains 2.0. The slope is greater for the tibiotarsi for AL, PB, HB, LL, and MF, whereas it is less for AN, PS, SF, CH, SW and NP. The slopes are almost equal for PS and NP, differing by less than 0.01.

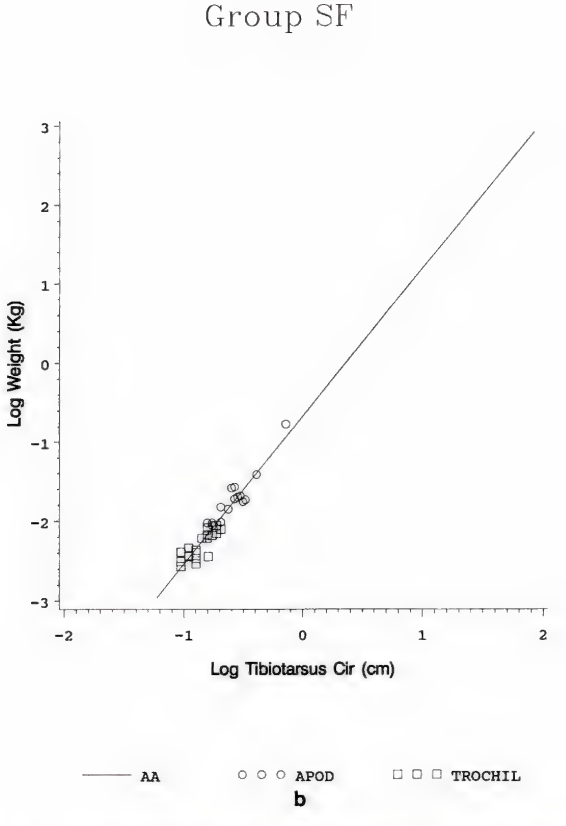
The pattern for the Anseriformes (AN) fits a compressive model best, as indicated by a less steep trend of data points, whereas the steeper trend of the data points for the predators (PB) is very close to the bending model. However, when we examine in even more detail those groups for which we have enough data, there are more subtle differences and trends. For example, among the Anseriformes (AN) we found that several small subgroups came close to the bending model, whereas the group as a whole more closely follows a compressive model. There is insufficient data, however, to test trends in the subgroups of Anseriformes.

A plot of AN and PB together (Fig. 9) shows how different the weights are for two groups of birds with overlapping hindlimb bone circumference ranges. The two patterns intersect for larger weights and circumferences. The differences in intercepts indicates that, for the same weight, smaller members of the group AN have smaller limb bones than the group PB. This suggests that the stresses borne by hindlimb bones in smaller members of the group AN are less than for group PB, which is not surprising because species in group PB are predators that capture prey with their feet. The additional stresses of prey capture with the feet, which can be expected to be significant, are not limited to the feet but are transmitted throughout the hindlimb structure.

This example points to some of the types of information that may be extracted from data sets such as ours. The summary plot (Fig. 8) of *rma*'s of all of our groups demonstrates their differing slopes and intercepts, and we suggest that a larger data base could prove a fruitful source for interpretive morphological studies. Unfortunately, although we have several hundred birds







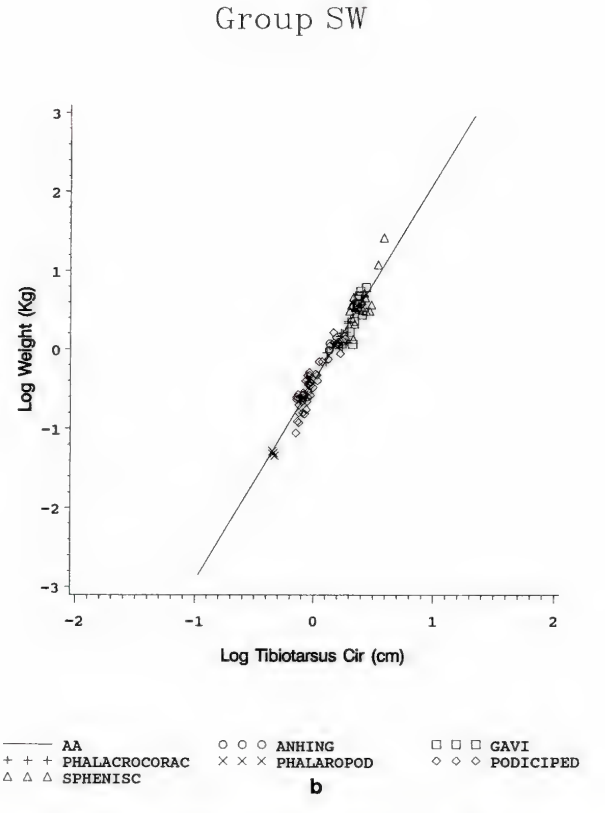
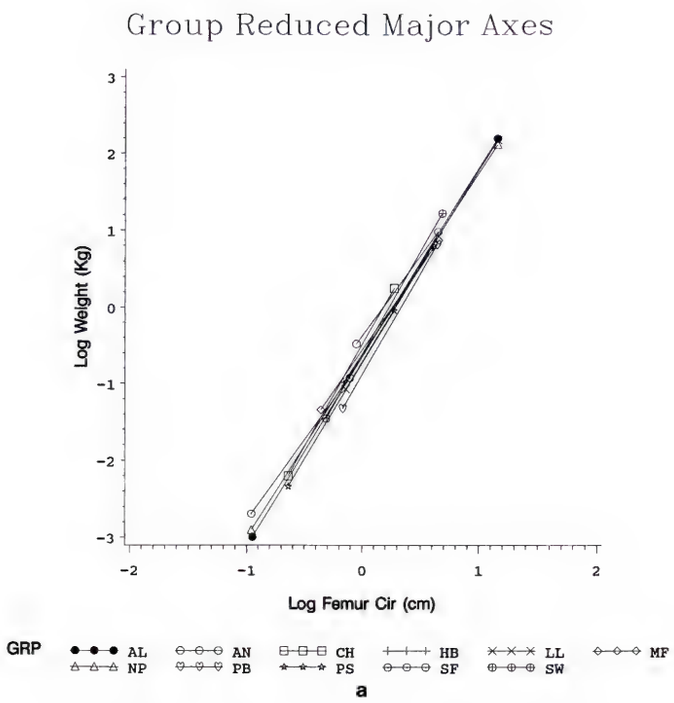


Figure 6. Plots of (**a**) $\log_{10}$(femur circumference) vs. $\log_{10}$(weight) and (**b**) $\log_{10}$(tibiotarsus circumference) vs. $\log_{10}$(weight) for subgroup **SF** (=small flyers of order Apodiformes).

Figure 7. Plots of (**a**) $\log_{10}$(femur circumference) vs. $\log_{10}$(weight) and (**b**) $\log_{10}$(tibiotarsus circumference) vs. $\log_{10}$(weight) for subgroup **SW** (=swimmers).



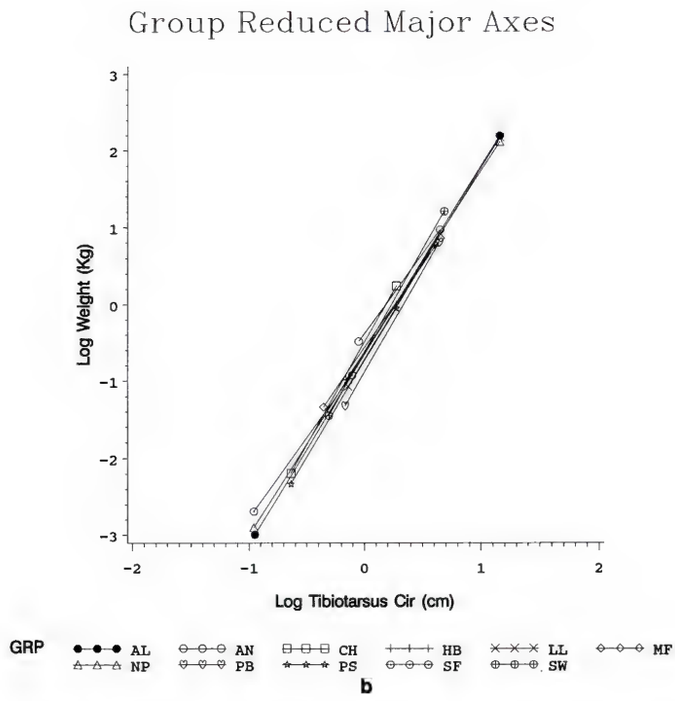
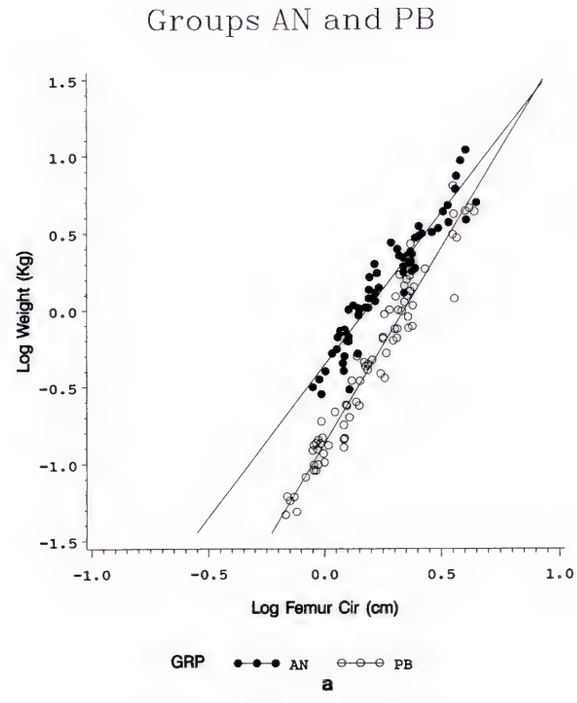


Figure 8. Plots of all subgroup reduced major axes (*rma*) of (**a**) $\log_{10}$(femur circumference) vs. $\log_{10}$(weight) and (**b**) $\log_{10}$(tibiotarsus circumference) vs. $\log_{10}$(weight).



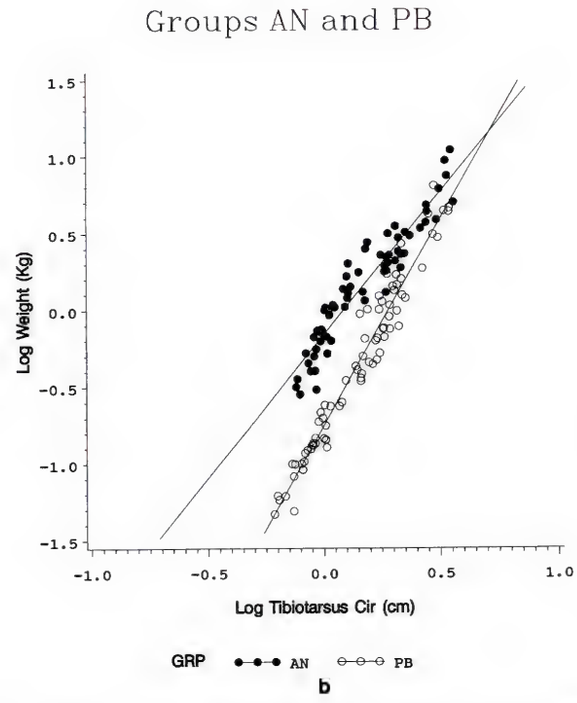


Figure 9. Plots of the regression lines for subgroups AN and PB of (**a**) $\log_{10}$(femur circumference) vs. $\log_{10}$(weight) and (**b**) $\log_{10}$(tibiotarsus circumference) vs. $\log_{10}$(weight). Small birds of the group AN have smaller hindlimb bones than birds of the group PB of the same weight, whereas the two groups become more similar as the individuals become larger.

in our overall data set, the numbers in subsets of the data are insufficient to extract conclusions with confidence.

Finally, the comparison of log femur to log tibiotarsus circumferences is largely consistent with an isometric slope of 1.0 (Table 2; Fig. 10). However, the long-legged (LL) group departs from 1.0 by more than 0.01 in its lower confidence bound, which means that in this group femur circumference increases faster for larger birds relative to the tibiotarsus than strict geometric scaling would predict.

Our data demonstrate diversity, but the broad band of points comprising our entire data set encompasses all of this diversity. Overall (AL), the bird data, with a slope of 2.5 for both femur and tibiotarsus, are closer to what we would expect if the bones were resisting bending more than compression (see Discussion). Our data tend to corroborate our interpretation of the bird femur as fulfilling its support function as a cantilever, rather than as a pillar.

DISCUSSION

If one accepts the premise that a primary role of the skeleton is to provide support for the rest of the body, and that it is this role that identifies a scaling model, then the skeletal elements that reflect body weight in birds are logically the three primary hindlimb bones: the femur, tibiotarsus, and tarsometatarsus. The bone in a bird's hindlimb that has the least variation in general form and structure from one kind of bird to another, particularly as regards its shaft structure, is the femur. The second least variable is the tibiotarsus. Of these two, the femur would appear to be the better indicator of body weight because its principal function is to provide static support for the bird's body weight. The tibiotarsus provides support for the body as well, but it also plays a more dynamic role in locomotion, and consequently its shape is often modified for its function.

The tarsometatarsus not only provides support and serves a locomotory function; it also often serves an important role in feeding. In this case, it may be much modified for a series of different functions. Cross-sections through the shaft of several tarsometatarsi of birds adapted to different locomotory and feeding strategies (Fig. 11) show that their structure is not readily comparable throughout the class, although it may be that within any given morphotype a constant relationship between some tarsometatarsal dimensions and body weight exists. Given the observed variety in form, it is difficult to identify a weak part of the shaft of tarsometatarsi in common to all members of the class.

ANALYSIS OF HINDLIMB FUNCTION

Support

To serve their support roles, the hindlimb bones must be sufficiently large to support the body without breaking, and include a safety factor (Alexander, 1981; Biewener, 1982, 1990), but yet not be so large as to be energetically too expensive to maintain. To understand why the femur and tibiotarsus have a close relationship to weight, it is necessary to examine how they perform their support function.

The hindlimbs must provide for total support on land, regardless of whether the bird is standing or perching or is in motion. Also, each leg must be strong enough to support the entire weight of the body because in many instances one leg may be involved in another activity and not provide any support. The forelimbs may be used to assist in support, but their modifications for flight or reduction to rudimentary status in flightless birds preclude them from a significant terrestrial support role.

In bipedal humans, the body is elongated vertically, hence its mass has its center of gravity concentrated over the hips. Bird bodies, however, tend to be elongated horizontally, and the center of gravity lies craniad to the articulation of the femur with the pelvis (Fig. 12; Gatesy, 1990: fig. 4). If a bird's legs attached to the body in a manner similar to that in humans, i.e., if the femora were in a vertical position, a bird would topple forward every time it tried to stand.

When a bird is standing at rest, the long axis of its femur is held at between 0° and 45° below the horizontal and generally much nearer the former than the latter (Fig. 12). This position was noted by Alexander (1975:358) when he stated that birds "... actually stand with their femur nearly horizontal ...." It is no accident that this position is also that seen in mounted museum specimens, fossil or Recent, and published illustrations of complete bird skeletons in works of all kinds.

When a bird is standing at rest, the sagittal (craniocaudal) axis of a bird's synsacrum is, as far as we can determine, never in a horizontal position. Rather, it varies from about 20° to 80° from the horizontal, depending upon the species. In general, the angle between the sagittal axis of the synsacrum and the long axis of the femur is much less than 90° and often less than 45°.

Unfortunately, in almost all illustrations of avian hindlimb anatomy in which the limb is illustrated apart from the rest of the bird, the longitudinal axis of the synsacrum is placed in a horizontal position. This places the femur into a nearly vertical position, which is quite unnatural. Becoming accustomed to viewing the femur in this position can lead to misinterpretations of how it actually provides support for the body. For example, Clark and Alexander (1975:90) illustrated and analyzed hindlimb musculature as if the femur approached the vertical, whereas in film tracings of running quail (Clark and Alexander, 1975:93) they depicted the femur remaining fairly steady between 20° and 25° from the horizontal at different intervals in the stride. However, in the latter illustrations the sagittal axis of the synsacrum is at approximately the same angle to the horizontal, or about 20°–25°.

When the bird is standing at rest, then, the femur must function as a nearly horizontal beam, or cantilever, supported by the tibiotarsus at one end and in turn supporting the rest of the body via the pelvis at the other end (Fig. 13). A bird's leg is kept from collapsing by muscles and tendons, not because the hindlimb bones are stacked one on top of the other, pillar-fashion, as in humans. The femur experiences its greatest stress when it approaches the horizontal plane; therefore, its shaft must be large enough in minimal cross-sectional circumference so as not to break under the bending forces being exerted on its ends when in that position.

For similar reasons, the least circumference of the tibiotarsus should also reflect a bird's body weight. The tibiotarsus is usually held in a more vertical position than the femur, but it often approaches the horizontal when a bird is walking, running, jumping, taking off, or landing. One might suspect that because of its greater locomotory functions the tibiotarsus would not be quite as good an indicator of a bird's weight because it experiences a greater variety of forces than the femur. However, the plane of least shaft circumference still cuts a tubular shaft that would be subjected to considerable bending forces. Our results show that the correlation for tibiotarsus least shaft circumference vs. body weight is not quite as high as that for femur least shaft circumference vs. body weight for the combined data set (AL) (Table 2). The two correlations are, however, very close and that for the tibiotarsus is even stronger in some groups. Regression of least shaft circumferences of bird femora on the least shaft circumferences of tibiotarsi shows that they are even more highly correlated (Table 2; Fig. 1D) to each other than either is to weight. If you know the circumference of one of these two bones, you can predict that for the other with fairly high confidence, and the least shaft circumference of either can be a reliable indicator of the weight of a fossil bird.

For both the femur and tibiotarsus, the plane of least shaft circumference almost always passes through a hollow tube.

Table 2. Correlation coefficient squared (RSQ), intercepts (int) and slopes [with confidence intervals given as lower confidence limits (lcl) and upper confidence limits (ucl) for reduced major axes (*rma's*) for groups], slopes for major axis (*ma*), and general structural relation (*gsr*, uncorrelated errors), based on species means within groups weighted by sample size. Abbreviations: nb, number of specimens; ns, number of species; OLS, ordinary least squares regression.

Results for relation between $\log_{10}$(weight) and $\log_{10}$(femur circumference)

Group	nb	ns	RSQ	int	lcl	<	*rma*	<	ucl	lcl	<	*ma*	<	ucl	lcl	<	*gsr*	<	ucl	Cor *gsr*
AL	795	387	0.961	−0.118	2.415	<	2.463	<	2.512	2.449	<	2.498	<	2.510	2.411	<	2.460	<	2.510	2.458
AN	65	40	0.908	0.538	1.796	<	2.079	<	2.406	1.850	<	2.144	<	2.523	1.739	<	2.038	<	2.365	1.983
CH	88	37	0.957	−0.157	2.399	<	2.667	<	2.966	2.444	<	2.713	<	3.039	2.394	<	2.668	<	2.973	2.668
HB	82	39	0.969	0.110	2.131	<	2.268	<	2.413	2.155	<	2.293	<	2.445	2.121	<	2.261	<	2.407	2.240
LL	95	49	0.968	−0.216	2.316	<	2.499	<	2.695	2.346	<	2.529	<	2.737	2.310	<	2.496	<	2.695	2.494
MF	39	15	0.947	0.262	1.858	<	2.174	<	2.544	1.896	<	2.213	<	2.629	1.844	<	2.169	<	2.547	2.165
NP	656	319	0.952	0.002	2.315	<	2.371	<	2.429	2.354	<	2.412	<	2.473	2.309	<	2.366	<	2.425	2.358
PB	76	33	0.953	−0.516	2.420	<	2.632	<	2.865	2.425	<	2.681	<	2.933	2.425	<	2.643	<	2.883	2.668
PS	139	67	0.948	−0.233	2.309	<	2.499	<	2.705	2.355	<	2.549	<	2.772	2.305	<	2.500	<	2.712	2.500
SF	34	27	0.909	0.230	1.812	<	2.071	<	2.367	1.865	<	2.135	<	2.474	1.815	<	2.085	<	2.402	2.102
SW	100	35	0.973	−0.294	2.542	<	2.673	<	2.812	2.569	<	2.701	<	2.846	2.535	<	2.668	<	2.808	2.662

Results for relation between $\log_{10}$(weight) and $\log_{10}$(tibiotarsus circumference); ns and nb as above

Group	RSQ	int	lcl	<	*rma*	<	ucl	lcl	<	*ma*	<	ucl	lcl	<	*gsr*	<	ucl	Cor *gsr*
AL	0.947	0.007	2.438	<	2.494	<	2.552	2.485	<	2.544	<	2.605	2.439	<	2.492	<	2.551	2.489
AN	0.909	0.871	1.688	<	1.951	<	2.256	1.733	<	2.007	<	2.358	1.629	<	1.908	<	2.210	1.873
CH	0.927	0.103	2.243	<	2.573	<	2.953	2.310	<	2.647	<	3.082	2.234	<	2.576	<	2.973	2.581
HB	0.964	0.140	2.231	<	2.385	<	2.549	2.261	<	2.416	<	2.590	2.222	<	2.379	<	2.545	2.363
LL	0.967	−0.418	2.555	<	2.758	<	2.978	2.590	<	2.794	<	3.028	2.555	<	2.762	<	2.986	2.765
MF	0.912	0.344	1.827	<	2.238	<	2.742	1.888	<	2.309	<	2.917	1.783	<	2.216	<	2.728	2.188
NP	0.939	0.170	2.303	<	2.366	<	2.431	2.353	<	2.419	<	2.488	2.294	<	2.359	<	2.426	2.349
PB	0.964	−0.515	2.558	<	2.755	<	2.967	2.596	<	2.794	<	3.021	2.556	<	2.756	<	2.973	2.760
PS	0.944	−0.124	2.293	<	2.489	<	2.702	2.341	<	2.542	<	2.774	2.288	<	2.489	<	2.709	2.490
SF	0.916	0.440	1.721	<	1.956	<	2.223	1.764	<	2.007	<	2.309	1.722	<	1.966	<	2.249	1.967
SW	0.956	−0.004	2.423	<	2.582	<	2.753	2.463	<	2.626	<	2.808	2.418	<	2.581	<	2.755	2.580

Results for functional relation between $\log_{10}$(femur circumference) and $\log_{10}$(tibiotarsus circumference); ns and nb as above

Group	RSQ	int	lcl	<	*rma*	<	ucl	lcl	<	*ma*	<	ucl	lcl	<	*gsr*	<	ucl	Cor *gsr*
AL	0.990	0.051	1.003	<	1.013	<	1.023	1.003	<	1.013	<	1.023	1.003	<	1.013	<	1.023	1.013
AN	0.984	0.159	0.883	<	0.938	<	0.997	0.882	<	0.938	<	0.997	0.882	<	0.938	<	0.997	0.937
CH	0.983	0.097	0.903	<	0.965	<	1.030	0.903	<	0.964	<	1.031	0.903	<	0.965	<	1.031	0.965
HB	0.969	0.000	0.977	<	1.046	<	1.121	0.977	<	1.047	<	1.123	0.973	<	1.044	<	1.120	1.032
LL	0.984	−0.081	1.047	<	1.104	<	1.164	1.047	<	1.105	<	1.166	1.048	<	1.105	<	1.166	1.109
MF	0.965	0.037	0.906	<	1.029	<	1.170	0.904	<	1.030	<	1.174	0.901	<	1.027	<	1.168	1.010
NP	0.988	0.071	0.986	<	0.998	<	1.010	0.986	<	0.998	<	1.010	0.986	<	0.998	<	1.010	0.998
PB	0.981	0.013	1.002	<	1.052	<	1.104	1.002	<	1.052	<	1.105	1.002	<	1.052	<	1.105	1.055
PS	0.982	0.043	0.950	<	0.996	<	1.044	0.949	<	0.996	<	1.044	0.950	<	0.996	<	1.044	0.996
SF	0.950	0.101	0.856	<	0.944	<	1.042	0.852	<	0.943	<	1.044	0.853	<	0.944	<	1.044	0.942
SW	0.978	0.108	0.923	<	0.966	<	1.011	0.922	<	0.966	<	1.011	0.924	<	0.967	<	1.013	0.969

Results for all data to compare to Campbell and Tonni and for estimation purposes

	All data (n = 795)					Weighted species means (ns = 391)				
	OLS			*rma*		OLS			*rma*	
Model	RSQ	int	slope	int	slope	RSQ	int	slope	int	slope
Weight—femur	0.958	−0.065	2.411	−0.119	2.463	0.961	−0.069	2.414	−0.119	2.463
Weight—tibiotarsus	0.944	0.076	2.424	0.074	2.495	0.947	0.072	2.428	0.074	2.494
Femur—tibiotarsus	0.987	0.057	1.006	0.051	1.013	0.989	0.056	1.008	0.051	1.013

Table 2. Continued.

Table of means of $\log_{10}$ measurements based on all individuals

	Individuals				Unweighted species			
	nb	Femur	Weight	Tibio-tarsus	ns	Femur	Weight	Tibio-tarsus
AL	795	1.032	2.424	0.969	390	1.008	2.384	0.943
AN	65	1.262	3.162	1.262	41	1.247	3.123	1.155
CH	88	0.921	2.300	0.854	41	0.967	2.409	0.900
HB	82	1.183	2.793	1.112	40	1.196	2.806	1.126
LL	95	1.311	3.059	1.261	50	1.303	3.014	1.250
MF	39	1.329	3.151	1.255	16	1.188	2.901	1.120
NP	656	1.262	2.633	1.041	322	1.087	2.597	1.017
PB	76	1.194	2.629	1.142	34	1.242	2.762	1.183
PS	139	0.668	1.436	0.627	68	0.634	1.376	0.592
SF	34	0.346	0.947	0.259	28	0.338	0.927	0.251
SW	100	1.209	2.938	1.139	37	1.228	2.994	1.155

Biewener (1982:298) states that "... a 'hollow cylinder' characteristic of a whole bone has a larger second moment of area (I) than a solid rod, and will therefore resist greater bending loads." Bühler (this volume), citing Bock (1974), disagrees, saying that a solid rod is stronger than a hollow tube. Currey (1984: 103) illustrates that a hollow cylinder is the least mass solution to providing strength to long bones and that as a cylinder gets larger, its walls may become thinner and still provide an equal amount of support. Currey and Alexander (1985) discuss the complexities of the factors that determine the thickness of the walls of tubular bones. With only a few exceptions, our data show that the least shaft circumference of the femur is greater than that of the tibiotarsus. Although we have not measured the bone wall thicknesses, it is our qualitative judgment that femoral shaft walls are thinner than tibiotarsal shaft walls. We postulate that this is because bending moments are the greatest forces stressing the femur, in contrast to compressive forces, and that these occur when the femur is in the horizontal position. For the tibiotarsus, there are two periods when bending moments are high. One is when it is near the vertical and passing into the main propulsive phase of a stride, at a time when compressive forces would also be at their highest level. The other is in the course of landing, when significant compressive force generated by the impact is passed on to the tibiotarsus from the tarsometatarsus. This compressive force is much reduced before being passed on to the femur.

Another reason why all birds have somewhat similar relationships between their body weight and the least shaft circumference of their femur and tibiotarsus, regardless of their size, behavior, or style of locomotion, is because *all* birds lay eggs on land, and, hence, must spend some time, however limited, on land or some other hard substrate. This is true whether they spend almost all of their time in water, on the ground, or in the air. It is not possible to lay eggs successfully while in flight or while swimming. Regardless of how short is the period of time that a bird spends on land to nest, even if it were only minutes, the legs must provide support for the body.

Factors Determining the Location of the Center of Gravity

The maintenance of proper balance when you have only two legs for support and locomotion, instead of four, is an engineering design problem. Not only is it necessary to counteract laterally acting forces, but forward movement will tend to set up a rocking motion about a horizontal transverse axis of rotation determined by the point of articulation of the femora with the pelvis (Clark and Alexander, 1975). In birds, this rocking motion might seem to be accentuated by the fact that a bird's center of gravity is placed well anterior to the transverse axis of rotation.

Two different centers of gravity are germane to this discussion. One is the center of gravity of the entire animal, which is important only in certain specialized activities, such as floating upon or swimming in water. A second center of gravity is far more important: the center of gravity of the entire bird *minus* the legs distal to the articulation of the femur with the pelvis (Fig.

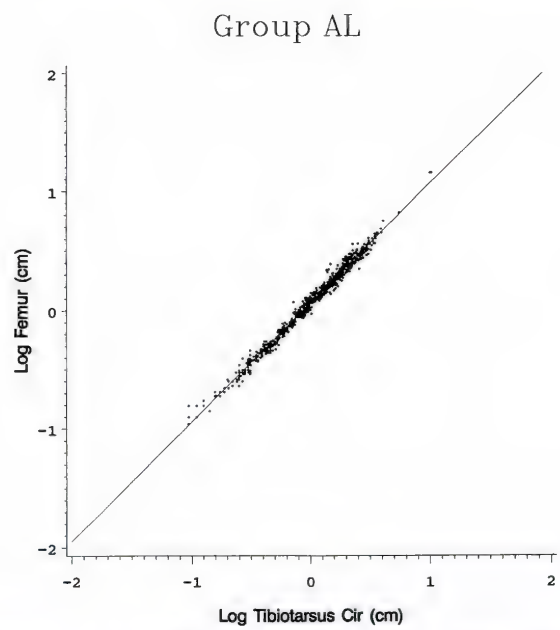


Figure 10. Plot of $\log_{10}$(femur circumference) vs. $\log_{10}$(tibiotarsus circumference) for 795 individual birds in 25 orders, 89 families, and 387 species.

Table 3. Ordinary least-squares regression estimates based on all individuals in each group. Abbreviations: int, intercept; RSG, correlation coefficient squared.

	All individuals			Species means (unweighted)		
	RSQ	Int	Slope	RSQ	Int	Slope
			Log_{10}(weight) vs. log_{10}(femur circumference)			
AL	0.958	−0.065–0.020	2.411–0.018	0.959	−0.018–0.027	2.382–0.025
AN	0.899	0.663–0.107	1.980–0.084	0.905	0.557–0.139	2.058–0.105
CH	0.950	−0.099–0.060	2.601–0.064	0.894	−0.128–0.143	2.624–0.141
HB	0.962	0.154–0.059	2.230–0.049	0.954	0.135–0.096	2.233-0.080
LL	0.955	−0.144–0.073	2.444–0.054	0.955	−0.173–0.102	2.446–0.081
MF	0.934	0.356–0.124	2.103–0.092	0.962	0.218–0.152	2.258–0.151
NP	0.949	0.070–0.024	2.310–0.021	0.951	0.115–0.033	2.283–0.029
PB	0.942	−0.414–0.089	2.548–0.073	0.971	−0.517–0.156	2.639–0.124
PS	0.936	−0.179–0.038	2.418–0.054	0.910	−0.138–0.061	2.387–0.092
SF	0.906	0.265–0.044	1.970–0.112	0.915	0.229–0.047	2.065–0.121
SW	0.963	−0.238–0.064	2.627–0.052	0.968	−0.280–0.107	2.665–0.092
			Log_{10}(weight) vs. log_{10}(tibiotarsus circumference)			
AL	0.958	0.076–0.022	2.424–0.021	0.942	0.140–0.030	2.380–0.030
AN	0.899	0.979–0.094	1.858–0.079	0.898	0.922–0.121	1.905–0.103
CH	0.920	0.187–0.068	2.702–0.077	0.828	0.224–0.162	2.427–0.177
HB	0.957	0.193–0.062	2.337–0.055	0.955	0.214–0.093	2.301–0.081
LL	0.953	−0.332–0.079	2.690–0.062	0.950	−0.384–0.114	2.717–0.090
MF	0.903	0.477–0.147	2.131–0.115	0.924	0.197–0.214	2.415–0.186
NP	0.935	0.250–0.026	2.289–0.024	0.937	0.312–0.035	2.274–0.033
PB	0.955	−0.442–0.079	2.690–0.068	0.937	−0.526–0.152	2.778–0.127
PS	0.935	−0.072–0.036	2.406–0.054	0.900	−0.021–0.060	2.361–0.097
SF	0.910	0.464–0.034	1.865–0.104	0.920	0.436–0.036	1.957–0.113
SW	0.944	0.079–0.072	2.510–0.062	0.930	0.091–0.138	2.514–0.117
			Log_{10}(femur circumference) vs. log_{10}(tibiotarsus circumference)			
AN	0.979	0.171–0.020	0.929–0.017	0.975	0.185–0.028	0.919–0.024
CH	0.978	0.106–0.013	0.954–0.015	0.960	0.117–0.028	0.944–0.031
HB	0.976	0.029–0.021	1.038–0.018	0.972	0.052–0.032	1.015–0.028
LL	0.977	−0.063–0.022	1.089–0.017	0.977	−0.070–0.031	1.098–0.024
MF	0.963	0.060–0.042	1.011–0.033	0.969	−0.002–0.058	1.062–0.051
NP	0.986	0.078–0.005	0.991–0.005	0.987	0.085–0.007	0.985–0.006
PB	0.963	0.019–0.027	1.029–0.024	0.971	0.017–0.038	1.035–0.032
PS	0.974	0.052–0.009	0.983–0.014	0.965	0.056–0.014	0.983–0.014
SF	0.948	0.108–0.012	0.919–0.038	0.941	0.108–0.014	0.915–0.045
SW	0.969	0.127–0.020	0.919–0.038	0.963	0.142–0.039	0.941–0.031
TO	0.987	0.058–0.004	1.006–0.004	0.988	0.064–0.006	1.002–0.006

12). It is the portion of the body minus the legs that is balanced about the horizontal transverse axis running through the heads of the femora and supported by the hindlimb skeleton. It is this weight that the femora must support when the bird is standing, whereas the tibiotarsi must support that weight plus the hindlimb weight proximal to it. When the bird is supported by one leg only, the mass of the second leg must be considered in determining this second center of gravity. The close relationship between femoral least shaft circumference and body mass throughout the Class Aves suggests that the percentage of total body mass comprising the legs is relatively consistent throughout the class. On the other hand, some of the differences in the observed slopes among our several groups of birds might in fact be related to differences in this percentage.

The center of gravity of a bird body *minus* the hindlimbs is, of course, located farther craniad than the center of gravity of the whole body. At first glance, this would appear to destabilize a bird because of the increase in the moment arm about the transverse axis of rotation. A bird maintains its balance and does not topple forward because the distal ends of the femora are at or slightly anterior to its center of gravity. The larger the bird, the farther the center of gravity is from where the femora attach to the pelvis and the longer the femora must be in order to extend under it. This explains the observed relationship between the length of the femora and the weight of the bird (Prange et al., 1979). If the distal ends of the femora were to extend posterior to the center of gravity, the bird would become unstable. From this consideration alone one can predict that the arc that the femur passes through when the bird is walking or running must be very limited.

Nonetheless, with the center of gravity located well anterior to the transverse axis of rotation it could prove to be energetically very expensive to control the dorsoventral rocking motion about this axis. This motion may be checked, i.e., dampened

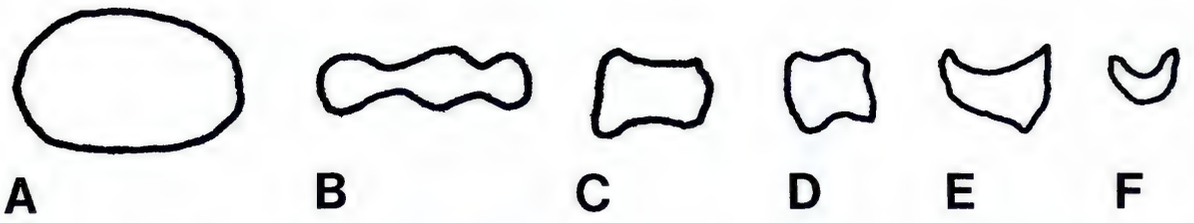


Figure 11. Cross-sections through the tarsometatarsi of several different groups of birds show the wide variety in their structure. Sections are taken in plane of least width, which does not always coincide with plane of least depth. **A,** Ostrich, *Struthio camelus;* **B,** King Penguin, *Aptenodytes patagonicus*; **C,** California Condor, *Gymnogyps californianus;* **D,** Marabou Stork, *Leptotilus crumeniferus;* **E,** Golden Eagle, *Aquila chrysaetos;* **F,** Great-horned Owl, *Bubo virginianus.* 1×.

or absorbed, by the femoral-pelvic musculature or in the small vertical movements of the distal end of the femur.

If bird legs were centered under their body so that the femora could be held vertically, this would eliminate some of the problems associated with the anterior–posterior rocking moment caused by having the center of gravity anterior to the transverse axis of rotation. However, when the first birds started flying, two mechanical adaptations had to evolve. One was getting as big a boost into the air as possible before they began to flap their wings, and the other, which is perhaps more important, was overcoming or absorbing the impact of landing. Birds accomplish both of these functions by maintaining their leg bones in an approximate Z-configuration, when viewed from the right. This configuration serves as a hinge-shaped mechanical spring that provides acceleration for jumping and shock absorption for landing.

Some terrestrial birds, especially those with long legs, may hold their lower leg bones in more of a vertical position when standing or walking, reverting to a Z-configuration only on landing or taking off. It appears that for standing or walking in very long-legged birds a more vertical configuration of the distal leg bones is best, but for landing and taking off the Z-configuration is required. Biewener (1989) claimed that birds show a shift to a more "upright" limb posture as size increases, analogous to that seen in mammalian quadrupeds. There are many small birds, e.g., thickknees and stilts, however, that have their lower legs as "upright" as an ostrich.

Birds cannot bring food to their mouths with their forelimbs, so they must take their mouths to food. Because food is seldom at the same horizontal level as their mouths, this often requires much dorsoventral rocking of the body about the transverse axis of rotation. If control over this motion were the sole factor determining where the center of gravity should be located, it would be on the transverse axis of rotation, thereby balancing the body on the axis of rotation and minimizing the effort required to feed. However, if a Z-configuration of the leg bones is required for landing and taking off, having the center of gravity over the transverse axis of rotation would increase the moment arm about the femur–tibiotarsus joint, thereby increasing the bending movement on the femoral shaft. Upon landing, with the center of gravity over the femur–tibiotarsus (knee) joint, forward rocking about the transverse axis of rotation reduces the bending moment on the femoral shaft by allowing the force of impact of landing to be absorbed over time. Absorption of the energy of impact is thus distributed not only through the braking action of the hinged joints of the leg bones, but also through the musculature associated with the femur over the length of the synsacrum.

Storer (1971) argued that in bipeds the center of gravity must lie over or between the feet. He suggested that this should lead to tibiotarsi and tarsometatarsi of nearly equal length in long-legged birds with small feet, which would enable the bird to go from a standing position to a sitting position without losing its balance. Alexander (1983a) disagreed, pointing out that few birds have tarsometatarsi equal in length to their tibiotarsi. He went on to suggest that the center of gravity of a standing bird is not in the same place as in a sitting bird. This may be true for the whole body center of gravity, but the center of gravity of the bird minus the hindlimbs, which is what must be balanced, is not displaced. He then went on to suggest that birds with very short tarsometatarsi shift their femora from a near vertical to a near horizontal position when going from a standing to a sitting position. Because birds do not hold their femora vertically while standing, as he himself has noted, and the projected range of movement is outside the physical capabilities of femora, it must be questioned if indeed the center of gravity must be located over the feet.

We think not, although having the center of gravity over the feet would certainly seem to be the most energy-efficient and stable positioning. But because the leg bones provide support in turn to each more proximal bone and in the end to the main body mass as cantilevers, it is not necessary that the center of gravity be positioned directly over the support base on the ground. It is only necessary that the most proximal segment of the cantilever system providing support, in this case the knee joint, be positioned under the center of gravity, which is what we observe

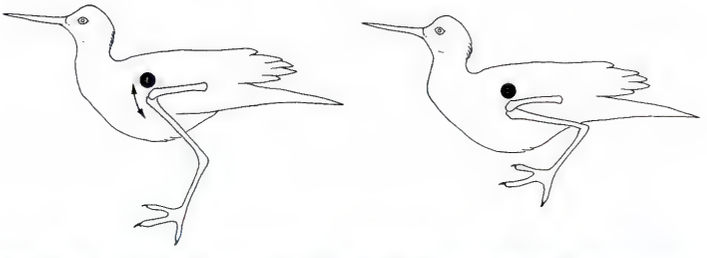


Figure 12. A bird's femora support the bird's weight at the point where their proximal ends articulate with the pelvis, but the bird's center of gravity lies forward of this point. Consequently, the femur is normally held near a horizontal position so that its distal end always remains under the center of gravity, thereby allowing the bipedal animal to maintain its balance. The double-headed arrow indicates the small arc through which the femur can move, an arc that keeps the distal end of the femur under the center of gravity. When a bird squats in preparation for jumping, the Z-configuration of the leg bones compresses, an action that provides the bird with greater "spring" in lift off.

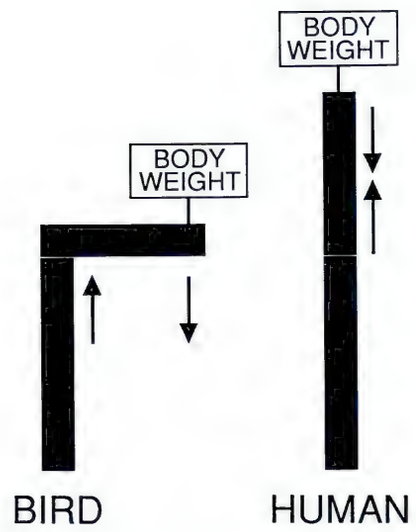


Figure 13. Diagrammatic view of the femur and tibiotarsus of a bird illustrating the origin of the bending moments stressing the femur. The femur acts as a cantilever, supporting the weight of the bird at its proximal end while being supported in turn by the tibiotarsus at its distal end. In contrast, animals that hold their leg bones in a vertical position experience compressive forces on the femur. Bending and compressional forces affect bone in different ways, so femora designed to withstand one type of force may not be able to resist breaking under an equal amount of the other type of force.

to be the case. This positioning does require, of course, a constant energy expenditure through the musculature to maintain the cantilever structure and provide for balance, but the only alternative is to position the center of gravity over legs that have a pillar-like structure, which apparently is inappropriate for birds.

Locomotion

As observed by Cracraft (1971), Clark and Alexander (1975), Alexander et al. (1979), and Gatesy (1990), the movement of the femur about the acetabulum during walking or running is, in the birds they studied, very small; therefore, the leg swings from the knee joint. This means that during periods of rapid locomotion the femur is passing up and down in a small arc (Fig. 12) as the bird moves through its gait. This limited degree of movement holds for large cursorial birds, such as the ostrich, as well as for the small birds these authors studied.

That this is true for ostriches was demonstrated experimentally by Fedak et al. (1982) when they analyzed the kinetic energy of limb segments in running ostriches. They illustrate graphically (Fedak et al., 1982: fig. 1) just how little the femur moves by showing that in a striding ostrich the upper leg segment (femur and associated musculature, which comprises by far the bulk of the mass of the whole leg) possesses only a very minimal percentage of the total internal kinetic energy of the leg. Most internal kinetic energy of the leg in running animals is associated with backward and forward movements of the leg (Alexander, 1984; Fedak et al., 1982), so the conspicuously small amount of observed internal kinetic energy in the upper leg segment can only mean that it moves very little in a striding ostrich. These experimental results can be supplemented through qualitative direct observations as well as in photographs of ostriches (e.g., Chadwick, 1983). It is the middle and lower leg segments, comprising the tibiotarsus, tarsometatarsus, and foot, that move back and forth when a bird is walking or running.

Gatesy (1990) documented that the femur has an excursion of about 5° during slow walking in *Numida* Linnaeus 1766 and suggested that this excursion increases to about 50° during running. He does not, however, indicate whether or not the latter figure takes into account the dorsoventral rotation of the synsacrum about the transverse axis of rotation at the point of maximum excursion. This rotation may account for a significant portion of the 50° "excursion" of the femur.

Another clue to the fact that a bird's femur does not move through a significant anteroposterior arc is the large mass of associated femoral musculature that must be moved with it. It is a widely recognized aspect of vertebrate anatomy that in swinging limbs the limb musculature is concentrated proximally as much as possible to reduce the moment of inertia about the various hinge joints in the limb (e.g., Hildebrand, 1987). However, a comparison between the location of the major propulsive muscle masses of the avian wing with those of the avian leg shows a considerable contrast. Either the femur does not move much in locomotion or the adaptive advantage of reducing its associated muscle mass for locomotion is outweighed by some other, currently unrecognized functional requirement. Additionally, it should be noted that for a femur to swing through an anteroposterior arc as large as commonly depicted, i.e., from the horizontal to posterior to the vertical, would require that some of its associated musculature elongate far beyond what is physically possible.

PREDICTING WEIGHTS OF FOSSIL BIRDS

Using the mathematical equation based on all birds derived from the expanded data set gives a predicted weight of 71.9 kg for *Argentavis magnificens*, compared to the original estimate of 78.8 kg (Campbell and Tonni, 1983). We consider the difference of 6.9 kg (9 percent) between the two estimates to be an acceptable result.

Using this equation, we also attempted to estimate the weights of some other fossil birds, including the Dodo, Elephant Bird, and two moas. The predicted weights, based on measurements of the femora, ranged from 13.2 to 16.4 kg ($x = 14.26$ kg, $n = 3$) for the Dodo, *Raphus cucullatus* (Linnaeus 1758). Measurements from eight femora of the Elephant Bird, *Aepyornis maximus* Geoffroy Saint-Hilaire 1851, which had a very stocky build, gave results of 333–663 kg ($x = 526$ kg). Two specimens of the largest known moa, *Dinornis maximus* Owen 1867, gave results of 245 and 299 kg. Estimates based on two specimens of *Pachyornis elephantopus* (Owen 1856), perhaps the most heavily built moa but considerably shorter in stature than *Dinornis maximus*, ranged from 180 to 211 kg. If, instead of the regression equation based on all birds, the species means are used, a slightly smaller value for the estimates is obtained.

There is still room for error in our estimates of the weights of these fossil birds. If *Argentavis magnificens* were a much smaller bird, we would have greater faith in the estimate of its weight because there are very few species of very large flying birds living today and they are not well represented in our data. We suggest that if such data were available and added to what we already have, our estimate of the weight of *Argentavis magnificens* would be greater than that currently predicted because the prediction equation now available is based mainly on small birds. The weight estimates for the Elephant Bird and the two moas would be greatly enhanced if data for the largest living

birds that approximate their body build, the ratites, were available. Unfortunately, these data are very rare.

Comparisons with Previous Weight Estimates for Fossil Birds

Alexander (1983a) estimated the body masses for moas by using four different techniques, none of which correspond to that used here. It can be seen (Table 4) that our estimates fall within the high and low estimates of Alexander (1983a) for *Dinornis*, whereas our estimates for *Pachyornis* were slightly higher. In later papers, Alexander (1985b, 1989a) looked at *Pachyornis* again, posing the question of why its leg bones were so massive compared to those of *Struthio*. Because his plot of moa tibiotarsi diameter falls right on the regression line he presents for flying birds, we find that the logical conclusion is that the log bone diameters scaled appropriately for the weight of the bird. *Pachyornis* had massive leg bones because for its stature it was simply a very heavy bird.

This conclusion is supported by the fact that much of Alexander's work (e.g., 1979, 1985) was based on conclusions drawn from an ostrich that weighed 41.5 kg. In contrast, Anderson et al. (1985) gave weights for two ostriches as 80.9 kg. Amadon (1947) used 100 kg as an average weight for ostriches, although he quotes a source as saying ostriches weigh about 136 kg. The weights of the two ostriches in our sample were 138 and 161 kg, more than the 137 kg average estimate of Alexander (1985) for the body mass of *Pachyornis elephantopus*. This large range in size in the ostrich makes it obvious that much larger data sets are required for this species before we can safely interpret any aspect of its functional morphology or energetics.

Amadon (1947) estimated the weights of *Dinornis* Owen 1843a and *Aepyornis* Geoffroy Saint-Hilaire 1851 by using proportions based on body length vs. weight and the cross-sectional area of the femoral shaft in the plane of least shaft circumference vs. weight of these extinct birds, relative to comparable proportions in living ratites. His results (Table 4) show some similarity to ours, although it should be noted that his weight estimates represent a mean figure for an unspecified number of individuals, whereas our estimates are for individual specimens. When viewed so, his estimate of 438 kg for *Aepyornis* is considerably less than the mean based on our eight specimens (526 kg).

Anderson (1989) reviewed weight estimates for moas and summarizes attempts by several authors to arrive at these estimates. His preferred weight estimate of 105 kg for *Pachyornis elephantopus* is much lower than what we give above, but it was derived in roughly the same manner; i.e., it is based on the cross-sectional area of the femur. We have not seen the original source for this figure (Smith, 1985), so we do not know the method used or the data upon which the estimates were based. He did not provide a new estimate for *Dinornis maximus*, which he synonymized with *D. giganteus* Owen 1843.

Table 4. Some weight estimates (kg) of large, extinct birds from different sources.

	Amadon (1947)	Alexander (1983)	From our femur regression equation
Aepyornis maximus	418, 457 x = 438	—	333–725 x = 542 n = 8
Dinornis giganteus	242	—	—
Dinornis maximus	230	—	255–300 x = 278 n = 2
Dinornis sp.	—	179–304 x = 231	
Pachyornis elephantopus	—	115–163 x = 137	143–211 x = 177 n = 2
Raphus cucullatus	—	—	13.2–16.5 x = 14.3 n = 3

PREDICTING WEIGHTS OF BIPEDAL DINOSAURS

Anderson et al. (1985) estimated the weight of bipedal dinosaurs using a scaling equation derived from the relationship between femur mid-shaft circumference and live body weight in birds, based on a data set of 126 birds. The results obtained by using our scaling equation and the circumference measurements provided by Anderson et al. (1985: table IV) are presented in Table 5.

The validity of using scaling relationships from birds to estimate the weight of bipedal dinosaurs is by no means established. First, the data set drawn from birds is at the small end of the bird–dinosaur size spectrum, with only a few ratites at the upper size limit of birds and lower size limit of dinosaurs at that. The assumption that the observed scaling relationship would hold to the size of an animal as large as *Tyrannosaurus rex* Osborn 1905 simply cannot be supported with the available data. If we must present estimated weights of large extinct ratites with pleas for caution, these caveats must be reinforced for the estimates for weights of dinosaurs.

A fundamental problem is the stance of bipedal dinosaurs. The location of a bird's center of gravity is well anterior to the transverse axis of rotation, and we have presented the hypothesis that this location is an adaptation to avian locomotion. It seems fairly clear from observations of reconstructed bipedal dinosaur skeletons that their centers of gravity are also located well anterior to the transverse axis of rotation, even taking into consideration their long tails. Regardless, bipedal dinosaurs are often illustrated with their hindlimbs stretched out behind them as if their center of gravity were at or posterior to the transverse axis of rotation (e.g., McMahon and Bonner, 1983:126), an impossible pose. Of course, it is possible to conclude that the center of gravity is located at or near the transverse rotational axis if its location is determined by suspending complete models of dinosaurs by strings, as is commonly done (Alexander, 1985a, 1989b). However, as mentioned earlier for birds, the legs must be discounted in determining the center of gravity for purposes of analyzing balance in locomotion. And if a model dinosaur were used to determine the center of gravity that had the hindlimbs stretched out behind them, as most do, then it would be concluded that the center of gravity was even farther posterior from its true position than if the legs were in their correct position.

Paul (1987:12) admits that bipedal dinosaur knees were very bird-like and that the femur never retracted past the vertical, although he then goes on to illustrate the femur of *Albertosaurus* swinging well past the vertical (Paul, 1987: fig. 5). In the same illustration, he depicts femoral movement in an ostrich that is unnatural, despite his express claim to the contrary.

Table 5. Weight estimates for some bipedal dinosaurs in comparison to those of Anderson et al. (1985). Circumferences for femora from Anderson et al. (1985).

	Femur circumference (mm)	Estimated weight (kg)	
		From Anderson et al. (1985)	From our femur regression equation
Parkosaurus warreni (Hypsilophodontidae)	103	50	61
Struthiomimus altus (Ornithomimidae)	136	110	120
Thescelosaurus garbani (Thescelosauridae)	201	310	308
Ceratosaurus nasicornis (Ceratosauridae)	267	670	610
Allosaurus fragilis (Allosauridae)	348	1,400	1,155
Hypacrosaurus altispinus (Hadrosauridae)	400	2,000	1,616
Edmontosaurus regalis (Hadrosauridae)	504	3,800	2,822
Anatosaurus copei (Hadrosauridae)	512	4,000	2,931
Tyrannosaurus rex (Tyrannosauridae)	534	4,500	3,244

We think it is probable that the femora of bipedal dinosaurs were held in a more horizontal position than normally depicted, that the anteroposterior movement of the femur was restricted to a small arc, and that the distal end of the femur certainly never moved posterior to the vertical plane. In other words, the functional morphology of the hindlimbs of bipedal dinosaurs was essentially avian. Padian and Olsen (1989) arrived at a similar conclusion by comparing footprints of ratites and theropod dinosaurs. As in birds, the leg probably swung from the knee joint and not at the hip. If bipedal dinosaurs had an avian-like knee joint, it is logical to assume that it functioned in a similar manner. However, because dinosaurs did not fly, the selective pressure exerted by the need to jump for lift-off or to cushion landing did not exist, so the adaptive advantage of a Z-configuration of the hindlimb bones to meet this need did not exist. This being the case, it is possible that the femora of bipedal dinosaurs were held closer to the vertical than in birds.

In this regard, it is noted that the femoral shafts in bipedal dinosaurs are usually arched dorsally as they are in birds (see also Padian, 1986:52). It is also noted that the more elongated the tarsals the more the femur appears to be arched dorsally. This suggests more of a cantilever-type of support system, as in birds, than a pillar-like support system, as in heavy quadrupeds where the femoral shafts are quite straight and the tarsals and metatarsals quite short. A particularly good example of this arching is seen in the femora of the ostrich dinosaurs. Russell (1972) presents a good review of some of these animals and attempts a reconstruction of their myology and life habits. Unfortunately, he based his analysis of cursoriality of the ostrich dinosaurs on comparisons with *Struthio* that assume that the femora of the latter are oriented in a vertical position and swings through a large arc, which we have shown not to be the case.

If the femora of bipedal dinosaurs were not held in a position similar to that seen in birds and were not similarly restricted in movement, then the use of scaling relationships derived from birds to predict their weight is not justified because the bending moments stressing the femora would not be the same. In this case, a different mathematical equation describing scaling based on femora would prevail. If the femora of bipedal dinosaurs were held and moved in a fashion after birds, then the use of the avian scaling relationship could be used to predict their weight. However, without a far larger data base drawn from living ratites, we cannot claim to really understand the avian scaling relationship and extrapolating to dinosaurs is risky at best.

SUMMARY AND CONCLUSIONS

An analysis of hindlimb bone dimensions and live body weight in 795 birds reveals that not all groups of birds fit the same scaling model. Overall, our data suggest that birds most closely approximate the model for elastic similarity. Nonetheless, some groups show values consistent with compressive similarity scaling, whereas another approached the value for geometric scaling. More data are required to assess scaling trends in different groups of birds with confidence.

We propose that the observed overall scaling relationship is a result of the functional morphology of the hindlimb, where the femur serves its support function as a cantilever and not a pillar, thereby being subjected more to bending moments than to compressive forces. The tibiotarsus is also subject to considerable bending moments, but it must also withstand greater compressive forces than the femur.

The center of gravity of a bird that is most important to balance during locomotion is that of a bird's body minus the hindlimbs. This center of gravity is found on the midline of the bird dorsal to the distal end of the femur, providing an explanation for the observed fact that the length of a bird's femur is related to its body mass; i.e., the larger the body, the farther the center of gravity is from the transverse axis of rotation and the longer the femur must be to support it. The whole body center of gravity is of much less importance in discussions of the functional morphology of the hindlimbs.

When birds walk or run, the distal ends of their femora move up and down in a small arc near the horizontal plane. It is the middle (tibiotarsal) and lower (tarsometatarsal + foot) limb segments that swing through an arc and define the stride of a bird.

Our data set allows a new estimation for the weight of *Argentavis magnificens*, the world's largest known flying bird, which is 71.9 kg [as opposed to 78.8 kg estimated by Campbell and Tonni (1983)]. Weights of other large extinct birds estimated on the basis of our data sometimes agree with earlier estimates, but in general they tend to indicate a larger size than previously estimated. The largest bird for which we have a weight estimate is a specimen of *Aepyornis maximus*, for which the estimate is 663 kg.

The use of estimation equations derived from birds to predict the weights of bipedal dinosaurs is a valid exercise only if bipedal dinosaurs had a hindlimb stance like birds. We conclude that the leg stance of some bipedal dinosaurs was similar to that of birds, i.e., that the femur served its support role as a cantilever and not a pillar, and that the closer the dinosaur hindlimb approaches that of birds in its proportions and femoral arching, the greater is this similarity. Bipedal dinosaur locomotion should be re-evaluated using the interpretations of avian functional morphology presented herein to eliminate misinterpretations

based on erroneous hypotheses of avian hindlimb stance and locomotion.

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MORPHOLOGICAL DIVERSITY OF PAST AND PRESENT NEW WORLD VULTURES

Fritz Hertel

ABSTRACT. Character divergence is expected in closely related sympatric species, especially where high species diversity exists. Analysis of vultures in the New World, both Pleistocene and Recent, demonstrates character divergence on the basis of three somewhat independent morphological characters: beak strength, body size, and body shape. These characters reflect feeding strategies, the effect of body size in interspecific encounters and resource partitioning, and habitat preferences. A comparison of late Pleistocene fossil vultures from Rancho La Brea, California, shows a diversity of beak strengths and body sizes similar to that observed in extant vulturid vultures.

RESUMEN. Se espera que especies emparentadas que viven en simpatría presenten divergencia de caracteres, especialmente si la diversidad de dichas especies es alta. Un análisis de buitres (Familia Vulturidae) del Nuevo Mundo pertenecientes al pleistoceno y reciente, demuestra dicha divergencia sobre la base de tres caracteres morfológicos casi independientes: fuerza del pico, tamaño corporal y forma del cuerpo. Estos caracteres reflejan estrategias de alimentación, el efecto del tamaño del cuerpo en encuentros interespecíficos y la repartición de recursos, y preferencias de hábitat. Una comparación entre buitres del pleistoceno provenientes del Rancho La Brea, California muestra una diversidad similar a la observada en vulturidos vivientes, en cuanto a fuerza del pico y tamaño corporal.

Key words: character divergence, guild, morphology, vulture.

INTRODUCTION

Vultures, all adapted to feeding on carrion, occur on every continent except Antarctica and Australia. Most species of vultures are sympatric with one or more other species of vultures throughout the greater part of their ranges, with some regions showing a high diversity, e.g., tropical South America and southern Asia. East Africa, where up to six species of vultures occur together (Brown and Amadon, 1968), has an exceptional diversity of these scavengers. Wherever vultures are sympatric, competition for available resources can be expected and character divergence in behavior, morphology, or both may result (Lack, 1971).

Extant vultures are represented by two geographically separated and taxonomically distinct groups: the Old World vultures and the New World vultures. The New World vultures of the family Vulturidae (=Cathartidae *auct.*) show close affinities to the ciconiid storks (Ligon, 1967; Rea, 1983; Olson, 1985). The Old World vultures of the family Accipitridae show close affinities to accipitrid hawks and eagles (Brown and Amadon, 1968). These two groups provide a classic case of convergent evolution in which phylogenetic effects are apparently minimal and morphological similarities are primarily the result of functional convergences between the Old and New World species. The abundant vulture remains found at the Pleistocene Rancho La Brea deposits of California provide a third group for analysis.

Kruuk (1967) studied six sympatric species of Old World vultures in East Africa and found ecological differences based on arrival times at a carcass, individual aggression, beak size, and body size. He determined three main groups of vultures with two species in each group. The first group comprised species with strong beaks that fed primarily on the tougher parts of a carcass such as skin and tendons. The second group comprised species with less powerful beaks that fed primarily on the softer muscle tissues. The third group contained the two smallest species, which have thin, weak beaks and generally picked up scraps from around a carcass. The latter two species were easily supplanted at a carcass by the larger species. Houston (1975) and Pennycuick (1972) showed further ecological differences within each group based on habitat preferences and flying abilities.

Behavioral interactions among New World vultures appear similar to those of the East African vultures. For example, more aggressive encounters occur between conspecifics or birds that feed on similar parts of a carcass. In East Africa, the two species of Griffon vulture [*Gyps africanus* Salvadori 1865 and *G. ruppelli* (Brehm 1852)] feed on the same parts of a carcass and are more likely to attack one another than they are to attack any other species of vulture (Kruuk, 1967). Similarly, Black Vultures, *Coragyps atratus* (Bechstein 1793), have a different feeding strategy from other vulturids and show more intraspecific aggression than interspecific aggression (Wallace and Temple, 1987; Houston, 1988).

The present study focuses on morphological diversity within the New World vulture guild during the Pleistocene and Recent. This guild, a group of species that exploits a similar resource in a similar way (Root, 1967), is here restricted to obligate avian scavengers of the family Vulturidae and two late Pleistocene accipitrid vultures from Rancho La Brea. The morphological diversity is based on three characters: beak strength, body size, and body shape. The first two characters reflect features that Kruuk (1967) found to vary among Old World vultures.

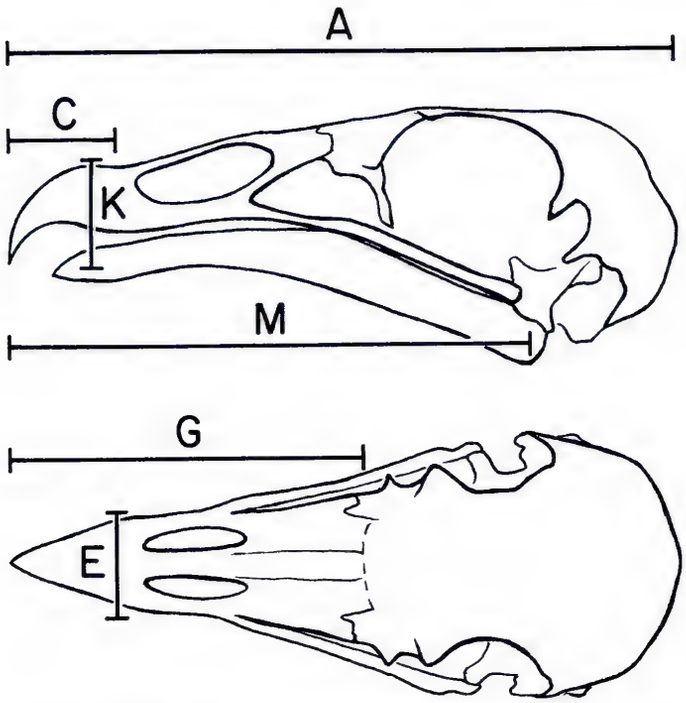

Figure 1. Beak index is calculated as beak size (beak length/skull length) × beak shape (beak length/beak width) × beak depth (C/A × C/E × K). Relative gape = gape length/beak length (M/G).

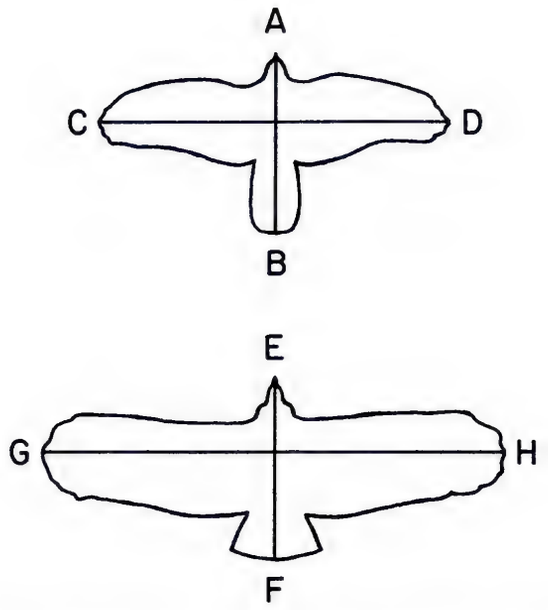

Figure 2. Body shape is calculated as ratio of wingspan : body length on study skins. A greater value (GH/EF > CD/AB) indicates a greater elliptical profile and generally a higher soaring altitude. Low elliptical profile shows a greater preference for more forested habitat.

METHODS AND MATERIALS

Measurements were taken with dial calipers (accurate to 0.1 mm) on adult specimens to determine differences among the following extant vulture species: *Vultur gryphus* Linnaeus 1758 (Andean Condor), *Gymnogyps californianus* (Shaw 1798) (California Condor), *Sarcoramphus papa* (Linnaeus 1758) (King Vulture), *Coragyps atratus* (Black Vulture), *Cathartes aura* (Linnaeus 1758) (Turkey Vulture), *Cathartes burrovianus* Cassin 1845 (Lesser Yellow-headed Vulture), and *Cathartes melambrotus* Wetmore 1964 (Greater Yellow-headed Vulture). The same measurements were taken on the Pleistocene vulturid species *G. californianus*, *Breagyps clarki* (Miller 1910), *Coragyps occidentalis* Miller 1909, and *Cathartes aura* and the accipitrid species *Neogyps errans* Miller 1916 and *Neophrontops americanus* Miller 1916 from Rancho La Brea. Specimens measured are housed in the following collections: Recent skins and skeletons, American Museum of Natural History, New York; Recent and fossil skeletons, Royal Ontario Museum, Toronto; Field Museum, Chicago; and Natural History Museum of Los Angeles County, Los Angeles; and fossil specimens, George C. Page Museum, Los Angeles.

ANOVA tests were performed on limb and skull elements of the different species to determine any significant size differences, and GT-2 tests were used to depict the results graphically (Sokal and Rohlf, 1981). Limb and skull characters were chosen for their presumed relationship to ecological differences involved with feeding, flying, locomotory ability on the ground, or correlation with body mass. These include indices of beak size and strength, relative gape, body shape, and body size.

The beak index (Fig. 1) was calculated using the following parameters:

1. Total skull length—the length of the skull from the maximum projection of the supraoccipital above the foramen magnum to the anterior tip of the beak.

2. Beak length—the length of the beak anterior to the anterior end of the external nares. This represents the portion of the beak with a tomium and is probably most involved with tearing food. Total beak length, measured from the nasofrontal hinge to the anterior tip of the beak, was also used to calculate the beak index, with similar results. However, tomium length probably reflects function more directly and is more likely to be preserved for fossil material.

3. Beak width—the maximum width just anterior to the external nares.

4. Beak depth—the maximum dorsoventral depth just anterior to the external nares.

The beak index was calculated by taking the relative beak size (beak length/total skull length) × the beak shape (beak length/beak width) × the beak depth (Fig. 1). Vulturids all have a similar beak design, so this index reflects relative beak strength independent of absolute beak size.

Relative gape was determined by taking the ratio gape length : beak length on study skins. The beak length was measured from the nasofrontal hinge to the anterior tip of the beak (Fig. 1).

Body shape was determined by taking the wingspan : body length ratio on modern study skins (Fig. 2) and from the literature (Table 1). This index cannot be derived for fossil taxa because it includes feathers.

Body size was estimated from femur length.

A three-dimensional diagram was constructed with three characters as axes: body size, beak strength, and body shape. All data used for this diagram are listed in Table 1.

RESULTS AND DISCUSSION

BODY SIZE

The log/log regression of body weight to femur length of both New and Old World vultures (N = 71 individuals of 11 species)

Table 1. Vulture data used in analyses. Headings and abbreviations: N, number of specimens; Feml, femur length (mm) (standard deviations in parentheses); body weight in grams; body weight references as follows: 1, Blake (1977); 2, Brown and Amadon (1968); 3, Brown et al. (1982); 4, predicted from regression in Fig. 3; beak strength and body shape data used in Fig. 5 (see text). *, fossils calculated without rhamphotheca, resulting in slightly different values.

Species	N	Feml	Body weight	Body weight references	Beak strength	Body shape
New World						
Vultur gryphus	9	148 (0.92)	11,750	1, 2	2.02	2.50
Gymnogyps californianus	9	135 (0.36)	11,120	1, 2	1.46	2.32
Sarcoramphus papa	9	100 (0.26)	3,375	1, 2	1.46	2.44
Coragyps atratus	10	86 (0.34)	1,560	1, 2	0.71	2.12
Cathartes aura	20	71 (0.31)	1,438	1, 2	0.92	2.03
Cathartes burrovianus	8	65 (0.36)	1,250	1, 2	0.59	2.30
Cathartes melambrotus	—	—	—		1.01	1.98
Old World						
Sarcogyps calva	2	107	4,550	2, 3		
Gyps fulvus	1	138	8,700	2, 3		
Necrosyrtes monachus	1	82	1,813	2, 3		
Torgos tracheliotus	1	132	6,700	2, 3		
Gyps africanus	1	103	5,981	2, 3		
Pleistocene, Rancho La Brea						
Coragyps occidentalis	10	97 (0.37)	2,315	4	0.35*	
Cathartes aura	7	73 (0.23)	1,409	4	0.49*	
Breagyps clarki	6	144 (0.68)	10,113	4	1.11*	
Gymnogyps californianus	9	149 (0.27)	11,166	4	2.15*	
Neophrontops americanus	10	80 (0.14)	1,838	4	0.34*	
Neogyps errans	8	107 (0.27)	4,273	4	1.50*	

has a coefficient (R^2) of 0.96 (Fig. 3). Tibiotarsus length and tarsometatarsus length are correlated to a lesser degree (R^2 = 0.94 and 0.83, respectively). Body size can, therefore, be estimated for fossil taxa with some confidence on the basis of femur length. Body size differences usually reflect important ecological differences (Schoener, 1984), e.g., size variation among vultures may determine dominance hierarchies at a carcass (Kruuk, 1967; Wallace and Temple, 1987). Moreover, larger vultures usually have a wider foraging range, are able to endure longer periods without feeding than smaller species, and usually have lower population densities.

Results of ANOVA and GT-2 tests indicate that the femur is the only limb bone element to show a distinct size segregation among extant New World vultures. No two extant species studied overlapped in femur size (Fig. 4). Other limb elements showed some size overlap, either in vultures of mutually exclusive ranges or in vultures of the same genus (Hertel, 1986). The femora of the late Pleistocene Rancho La Brea vulture specimens show a similar size segregation, although some species more closely approximate each other. This is true despite the presence of different species and the addition of two accipitrid vultures (*Neogyps errans* and *Neophrontops americanus*) (Fig. 4). It appears that sympatric vultures in the New World differ similarly in femur size, and presumably body size, in both Recent and fossil guilds.

The results of the ANOVA and GT-2 tests on femur length were used to construct the axis for body size in Fig. 5.

BEAK INDEX

This index was used to assess the relative beak strengths of the different vulture species. Relatively large, deep beaks have high values for the beak index and relatively small, narrow beaks have lower values (Fig. 1). *Gymnogyps californianus*, *Vultur gryphus*, and *Sarcoramphus papa* all have relatively stronger beaks than the smaller vultures (Fig. 5). This is expected because

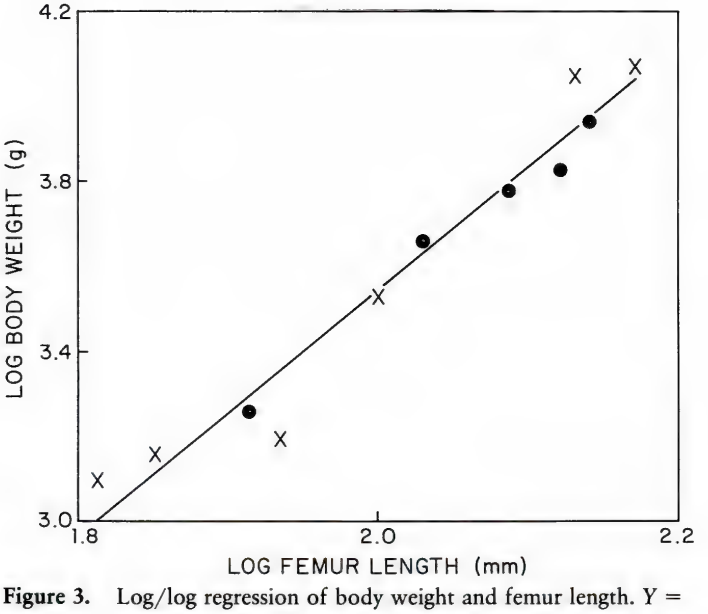

Figure 3. Log/log regression of body weight and femur length. $Y = 2.9X - 2.2565$, $R^2 = 0.96$, standard error of slope = 0.2094. Abbreviations: **X,** New World vultures; **O,** Old World vultures: *Gyps africanus, Necrosyrtes monachus, Gyps fulvus, Sarcogyps calva,* and *Torgos tracheliotus.*

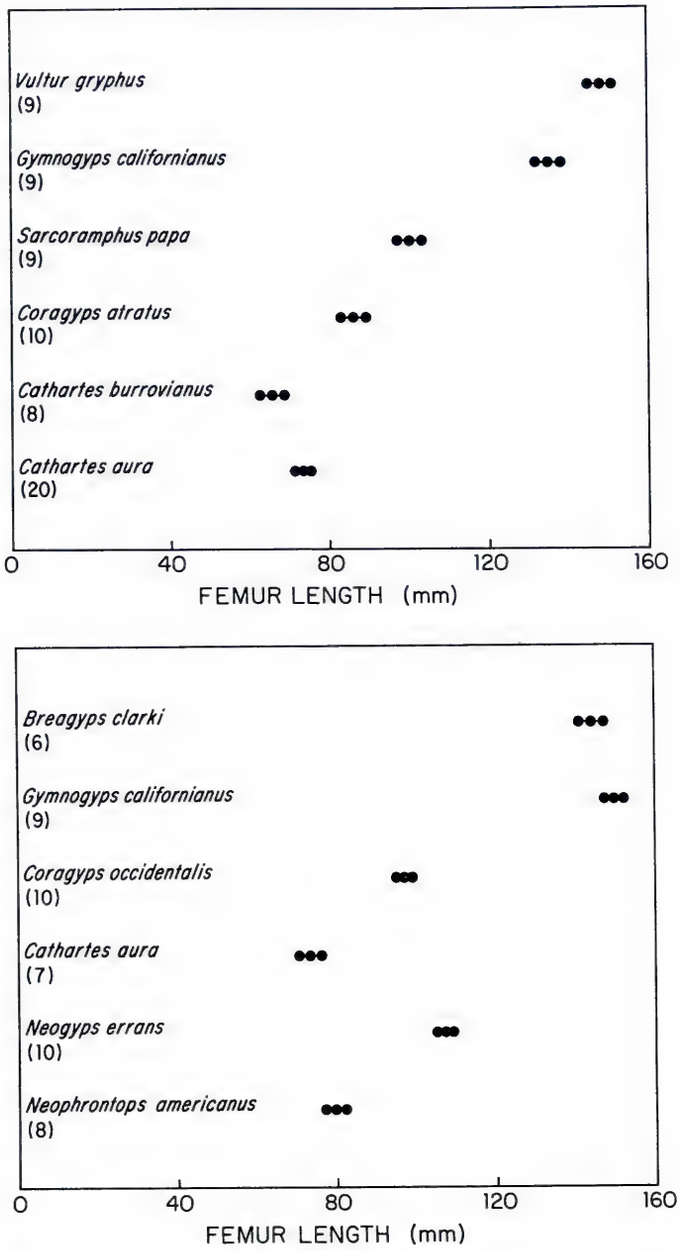

Figure 4. ANOVA and GT-2 results for femur lengths of extant New World vultures (top) and Pleistocene vultures at Rancho La Brea (bottom). Numbers in parentheses indicate numbers of individuals measured. Non-overlapping ranges indicate a significant difference at $P < 0.05$.

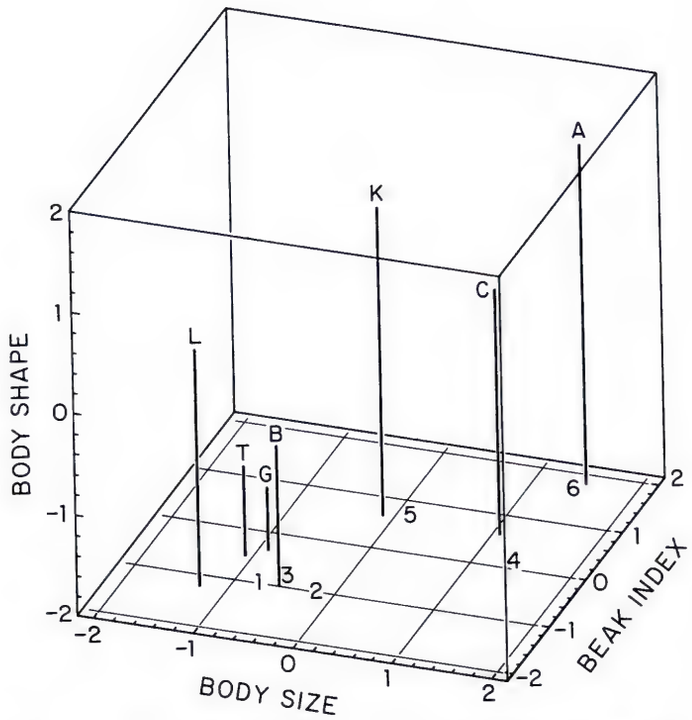

Figure 5. Morphological diversity in vulture guild of New World. Body size axis is based on femur lengths. A higher number for the beak index indicates a stronger beak. Higher values for body shape indicate a greater elliptical profile (wingspan : body length) and generally higher altitude soarers. All axes are plotted as standardized deviations of the mean. Abbreviations: **A,** Andean Condor (*Vultur gryphus*); **C,** California Condor (*Gymnogyps californianus*); **K,** King Vulture (*Sarcoramphus papa*); **B,** Black Vulture (*Coragyps atratus*); **T,** Turkey Vulture (*Cathartes aura*); **L,** Lesser Yellow-headed Vulture (*Cathartes burrovianus*); and **G,** Greater Yellow-headed Vulture (*Cathartes melambrotus*). Body size for G based on estimate of femur length. Numbers (**1–6**) represent fossil specimens at Rancho La Brea (**1,** *Neophrontops americanus;* **2,** *Coragyps occidentalis;* **3,** *Cathartes aura;* **4,** *Breagyps clarki;* **5,** *Neogyps errans;* and **6,** *Gymnogyps californianus*).

these large vultures are known to open carcasses of relatively large mammals such as tapirs and cattle (Eitnear, 1982). Individuals of *Cathartes aura* have relatively weak beaks and have been observed to arrive at an untouched carcass and not feed until the larger *S. papa* appears and opens the carcass (Eitnear, 1982). A small beak is perhaps better for manipulating smaller bits of food than for opening carcasses.

ANOVA and GT-2 tests on relative gape sizes (Fig. 6) suggest a relationship among feeding strategies, body size, and relative abundances of the vulturids. Larger vultures have relatively smaller gapes (Fig. 6), are relatively less abundant, and can supplant smaller species at a carcass. *Coragyps atratus* generally occurs in the highest densities wherever present and has the relatively largest gape. Behavioral and morphological adaptations for swallowing large amounts of food at any one time would be advantageous for vultures that normally feed in large groups because aggressive encounters are most numerous among conspecifics (Wallace and Temple, 1987). The larger vultures are less numerous and do not normally feed in large groups, so competition at a carcass appears to be less frequent.

BODY SHAPE

Body shape was determined by taking the wingspan : body length ratio (Fig. 2). All vulturids are of similar body design, so this index should reflect differences within this family; the numerical values for the index for this family are not applicable to interfamilial comparisons. A high value for body shape indicates a greater elliptical profile or a bird with a relatively long wingspan. Birds with long broad wings and relatively short tails are well adapted for soaring flight (Brown and Amadon, 1968). By contrast, birds with relatively short, rounded wings and relatively long tails are more manueverable and better adapted for a more

forested habitat. Thus, body shape appears to reflect aspects of habitat choice and flight behavior in birds. The three largest vultures (Figs. 5:**C, A, K**) show the greatest elliptical profile. *Gymnogyps californianus, Sarcoramphus papa,* and *Vultur gryphus* are more often observed soaring at greater altitudes than the smaller vultures (Grossman and Hamlet, 1964; Houston, 1988). *Coragyps atratus* has a greater elliptical profile than *Cathartes aura* and usually soars above *C. aura,* often using the latter as cues to locate food (Stewart, 1978). Of the vulturids, *Cathartes melambrotus* has the most rounded profile (relatively longer tail) and prefers more forested habitats (pers. obs.).

RECENT DIVERSITY

Extant vulturids appear to segregate by size and to show a range of beak strengths and body shapes associated with different feeding strategies and habitat preferences (Fig. 5). Within the guild, there are three large vultures with relatively strong beaks and elliptical body shapes (Figs. 5:**K, A, C**). Although these three vultures are all similar in body shape, no two are close in beak index and body size as well. For example, *Vultur gryphus* differs relatively little in body size from *Gymnogyps californianus* but differs greatly in beak index (Figs. 5:**A, C**). Similarly, *G. californianus* and *Sarcoramphus papa* are close in beak index but differ markedly in size (Figs. 5:**K, C**). The range of Recent *G. californianus* is outside those of these other two vultures, but fossil remains of two large, closely related vultures (*Geranogyps reliquus* and *Gymnogyps howardae*) have been found at the Pleistocene Talara Tar Seeps of Peru, along with *Vultur gryphus* (Campbell, 1979). The smallest vultures (Figs. 5:**B, T, L, G**) also appear to segregate along the three axes, but more finely than the largest vultures. The three species of *Cathartes* (Figs. 5:**L, G, T**) appear most similar of the four small species.

If the three species of *Cathartes* are analyzed as a group, there appears to be some character divergence. There were no skeletal limb elements available of *C. melambrotus,* so its predicted femur length (body weight) is estimated based on relative comparisons with the other species of *Cathartes.* The other two indices were calculable and are, therefore, plotted accurately. *Cathartes aura* is the most widespread and generalized in habitat choice of the three species and was also present during the Pleistocene in South America (Campbell, 1979). If *C. aura* is the ancestral form, then *C. burrovianus* and *C. melambrotus* have diverged from *C. aura* in different directions, which reflect behavioral differences and habitat preferences. *Cathartes burrovianus* has a weaker beak, more elliptical shape, and prefers open savanna habitat (Figs. 5:**L**). Conversely, *C. melambrotus* has a stronger beak, more rounded shape, and prefers relatively forested habitats (Figs. 5:**G**).

PLEISTOCENE DIVERSITY

The numbers (**1–6**) in Fig. 5 represent the fossil species at Rancho La Brea. Data on body shape are not available for the fossil specimens, so they cannot be plotted along the body shape axis. Despite the occurrences of different vulturid species and two unrelated accipitrid vultures, Pleistocene vultures scale similarly in femur size, and presumably body weight, to extant vultures with a comparable range of size. Some Pleistocene vultures appear to be closer in size to each other than do Recent vultures (Fig. 4), suggesting that the fossil vultures may have been partitioning their resources more finely.

The diversity of beak strengths during the late Pleistocene appears to be similar to that found in the Recent species. In both guilds, there are three vultures with relatively strong beaks

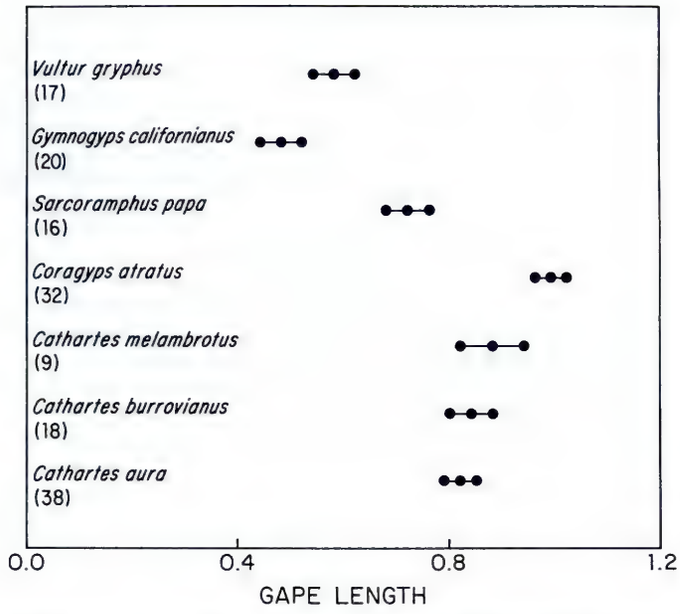

Figure 6. ANOVA and GT-2 results for relative gape lengths of extant New World vultures. Numbers in parentheses indicate numbers of individuals measured. Non-overlapping ranges indicate a significant difference at $P < 0.05$.

(Fig. 5; beak index > 0) and three with weaker beaks (Fig. 5; beak index < 0). This suggests that the Pleistocene vultures exhibited differences in feeding behavior that parallel those observed among Recent vultures. Results for beak strength (Fig. 5) indicate that for vultures of similar size, the one with the weakest beak became extinct. For example, *Breagyps clarki* (Fig. 5:**4**), which is close in size to *Gymnogyps californianus* (Fig. 5:**6**), had the weaker beak and became extinct. Similarly, *Neophrontops americanus* (Fig. 5:**1**), which is close in size to *Cathartes aura* (Fig. 5:**3**), had the weaker beak and became extinct.

At the end of the Pleistocene, selection appears to have favored those vultures that were able to handle large carcasses efficiently or the ability to locate carrion with a sense of smell. The ability of *Cathartes aura* to locate carrion by smell (Stager, 1964) has probably contributed greatly to the success of Neotropical avian scavengers because other vulturids frequently cue on *C. aura* to locate carrion (Stewart, 1978; Houston, 1988). *Cathartes* is clearly the most successful extant genus, suggesting that a sense of smell may have been a key adaptation after the extinction of large ungulates during the Pleistocene. This sense of smell may also be true for *C. burrovianus* (Houston, 1988) and for *C. melambrotus* (pers. obs.).

CONCLUSIONS

The New World vulture guild comprised a significant amount of morphological diversity, during both the Pleistocene and Recent, consistent with hypotheses of competition and character divergence. These results parallel Kruuk's (1967) findings with extant East African vultures, suggesting that despite differences in phylogeny vultures from varied geographical areas separate in similar ways, which reflect carcass-processing abilities and body size differences. This study independently supports Houston's (1988) conclusions concerning the similarity of feeding behaviors between the New and Old World vulture guilds.

There is a fair amount of available carrion in Neotropical forests (Houston, 1985), which would seem capable of accommodating a high diversity of scavengers. At the end of the Pleistocene, selection appears to have favored those vultures that were able to handle large carcasses efficiently or the ability to locate carrion with a sense of smell. No Old World vultures have been shown to locate carrion using a sense of smell and few occur in forested habitats.

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INTRASPECIFIC VARIATION AND THE IDENTIFICATION OF PLIOCENE AND PLEISTOCENE GREBES

Robert W. Storer

ABSTRACT. The increased knowledge of geographic and other variation in birds and large numbers of available skeletons of Recent birds make possible a better understanding of the fossils of the same or closely related forms. Examples from the grebe genera *Aechmophorus* and *Podilymbus* are used to show how some problems can be solved by analyses of this material.

Key words: fossil birds, intraspecific variation, Pleistocene, Pliocene.

INTRODUCTION

Many species found in Pleistocene deposits are still extant or have close living relatives. Hence, knowledge of variation in Recent species has become especially important in studying their Pleistocene representatives and, to a lesser extent because of smaller samples, late Pliocene fossils. It is therefore instructive to see how advances in the study of Recent species have been used in the study of these fossils.

The accuracy of statistical analyses depends to a large degree on sample size. Fortunately, some fossil forms are known from large numbers of nearly complete elements from single localities (i.e., Fossil Lake, Oregon, and several sites in Florida). It is thus possible to measure series of these fossils and to make statistical comparisons of these with series of Recent skeletons. The increase in numbers of skeletons of living species also makes possible analyses of geographic variation, some of it not hitherto recognized or not accurately described. I hope to show the importance of a background in geographic variation and large sample sizes in the study of fossil birds using the grebe genera *Aechmophorus* Coues 1862 and *Podilymbus* Lesson 1831 as examples.

Many of our most eminent paleontologists—E.D. Cope, R.W. Shufeldt, Loye Miller, Alexander Wetmore, Hildegarde Howard, and Pierce Brodkorb—have published fine works on fossil grebes. However, increases in our knowledge of the distribution and variation of Recent birds and the application of statistical analyses have changed our understanding of fossil grebes as well as our approach to other ornithological research and suggest that modifications of these earlier studies may be in order.

MATERIALS AND METHODS

Fossil and Recent material was measured to the nearest tenth of a millimeter with dial calipers. The Recent material consisted primarily of the extensive material in the University of Michigan Museum of Zoology, including examples of all Recent species of grebes except *Tachybaptus pelzelnii* (Hartlaub 1861) of Madagascar. In all, 331 skeletons of *Aechmophorus*, 254 of *Podiceps* Latham 1787, and 60 of *Podilymbus*, plus some additional borrowed material, were available.

Acronyms used for collections from which specimens were examined are as follows: RWD (Robert W. Dickerman), UMMP (University of Michigan Museum of Paleontology), and UMMZ (University of Michigan Museum of Zoology).

AECHMOPHORUS

The two Recent species of *Aechmophorus*, *A. occidentalis* (Lawrence 1858) and *A. clarkii* (Lawrence 1858), differ only in color and, to a limited extent, in behavior. In some places where they are sympatric, *A. clarkii* averages slightly smaller than *A. occidentalis* in some measurements, but there are no known characters by which skeletons of the two forms can be distinguished (B.C. Livezey and R.W. Storer, in prep.). Formerly considered color phases of the same species, they are now regarded as biological species. However, because of the impossibility of identifying skeletons of these two forms to species, I shall revert to the older nomenclature and refer to both as *A. occidentalis*, the Western Grebe, for the purposes of this paper. This continues the usage in earlier studies of the fossil *Aechmophorus*.

Fossils of the Western Grebe are abundant in the Pleistocene deposits of Fossil Lake and Silver Lake, Oregon, whence they were first mentioned by Cope (1889). Three years later, Shufeldt (1892) discussed these bones more thoroughly and, like Cope, referred them to the Recent species, although he mentioned a possible difference in the crest of the humerus. Loye Miller (1911) recognized two species of *Aechmophorus* in the Fossil Lake material: a smaller one, which he referred to the Recent species, and a larger one, which he named *A. lucasi* L. Miller 1911. The number of Recent skeletons used in all of these comparisons and where they were taken were not stated. Two years later, Shufeldt (1913) argued against the existence of two species of *Aechmophorus* in these deposits, suggesting that the differences found by Miller resulted from age, sex, or osteological changes since the Pleistocene.

In her exhaustive study of the Fossil Lake avifauna, Howard (1946) compared more than 800 fossil bones of *Aechmophorus*

Table 1. Measurements (mm) of study skins of Pied-billed Grebes (*Podilymbus podiceps*).

	North America[1]		West Indies		South America	
	n	Mean (SD)	n	Mean (SD)	n	Mean (SD)
Males						
Wing length (arc)	84	134.9 (3.92)	29	128.2 (5.18)	61	138.5 (4.67)
Tarsus length	94	42.00 (1.82)	29	41.81 (1.75)	62	43.87 (1.99)
Bill from nostril	91	15.13 (0.84)	29	15.27 (0.94)	58	16.27 (0.96)
Bill depth	71	12.26 (0.73)	21	11.78 (1.09)	44	12.79 (0.79)
Females						
Wing length (arc)	94	122.2 (3.44)	28	118.0 (3.49)	72	128.6 (3.80)
Tarsus length	105	37.97 (1.39)	29	37.89 (1.46)	74	40.54 (1.63)
Bill from nostril	101	12.99 (0.67)	28	13.14 (0.62)	76	14.22 (0.72)
Bill depth	86	10.27 (0.59)	19	10.15 (0.45)	50	11.19 (0.68)

[1] To, but not including, Panama.

with "seven or eight" Recent skeletons. She was convinced that a single species was represented in the fossil material and that this form averaged larger than the Recent form. This difference she expressed by using the trinomial, *Aechmophorus occidentalis lucasi* L. Miller 1911, as a "chronoclinal" subspecies. Her small sample of Recent specimens, however, did not show the range of geographic variation in size present in Recent Western Grebes.

Geographic variation in Western Grebes was first reported by Dickerman (1963), who found that birds from the Mexican Plateau were considerably smaller than those from the United States and Canada. This led to an analysis of geographic variation within the whole range of *Aechmophorus* based on measurements of study skins of adults taken on the breeding grounds (Storer and Nuechterlein, 1985). In this study, we confirmed the small size of the Mexican birds (of both color forms) and found a cline of increasing wing length from the southwestern United States to Canada.

To analyze the Fossil Lake material, I measured skeletons of 119 *Aechmophorus occidentalis* found frozen on a lake in Alberta. The results (unpubl.) showed that the males, like those of other grebes, were significantly larger than the females, and that the immature birds (in this case, approximately 6 months old) were smaller in some measurements, especially the widths of the ends of long bones, than the adults of the same sex.

After finding no obviously immature specimens in the material from Fossil Lake, I compared 10 adult males and 10 adult females taken in Canada with a large sample from Fossil Lake (Storer, 1989). In a few measurements, the Fossil Lake birds were slightly, but significantly, smaller (at least at the 0.05 level) than the Canadian birds. I also measured seven of the Recent skeletons from California used by Howard in her analysis. These consisted of one adult and two first-year males and two adult and two first-year females. Three of these birds came from Monterey and four from farther south.

As predicted from the analysis of geographic variation shown by study skins, the birds in Howard's sample proved significantly smaller than those in the Canadian sample. That the Oregon fossils are intermediate in size between the Recent skeletons from Canada and southern California fits the present clinal variation. Thus, the difference between Howard's Recent sample and the Fossil Lake birds is better explained as geographic, rather than chronologic, variation.

Brodkorb and Phillips (1973) reported on a coracoid of *Aechmophorus occidentalis* from Pleistocene deposits in the Valley of Mexico. This bone was "large, with a distal width [=width at sternal end] of 15.8 (14–15.0 in Recent males), least width of shaft 4.0 mm." The range and (mean) of these measurements of six coracoids of the small, resident Mexican population are distal width, 12.3–14.1 (mean, 13.3), and least width of shaft, 3.2–4.1 (mean, 3.65), and of 40 Canadian skeletons (10 each of adult and immature males and females), distal width, 13.6–17.4 (mean, 14.84; SD, 0.99), and least width of shaft, 3.6–4.7 (mean, 4.24; SD, 0.27). Thus, the Mexican fossil falls well within the range of the Canadian sample. It is also within the range of variation for Recent Mexican birds in shaft width, but, even if the range of variation for Recent Mexican birds is as great as that for the Canadian birds, the proximal width of the fossil would be above the upper extreme for that sample. Assuming that no size change has taken place since the late Pleistocene, the fossil is probably from a wintering bird from farther north, although it is possible that the fossil was laid down at a time when colder temperatures caused a southward shift in the populations of the species.

Pleistocene deposits from Lake Chapala, Mexico, have yielded 25 fragmentary fossils attributable to the Western Grebe. All are incomplete elements and almost impossible to measure. They include parts of five vertebrae, seven synsacra, two notaria, four sterna, three humeri, one femur, and three tarsometatarsi. As far as can be told by visual comparison, all but two are within the size range of the six available skeletons of the Recent Mexican population. The exceptions are the proximal ends of two tarsometatarsi that are considerably heavier than those of Recent Mexican birds. The Lake Chapala fossils are roughly contemporaneous with those from Fossil Lake and similarly were laid down over a fairly long period of time (G.R. Smith, pers. comm.). The larger tarsometatarsi, like the aforementioned coracoid, may either represent wintering individuals from the north or may have been laid down during a glacial advance when northern populations may have been shifted southward.

Aechmophorus elasson Murray 1967 was described from the Upper Pliocene (Hagerman) Glenns Ferry Formation of Idaho. The type consists of the distal end of a humerus and associated complete ulna. The latter was described by Murray (1967:282) as "considerably smaller than that of *A. occidentalis*" based on comparison with measurements of four males and five females of Recent specimens from the northern part of the species' range. However, the ulnae of two females from southern California (UMMZ 204,701 and 204,707) equal or approach the length of the type ulna (93.9 and 94.7 mm vs. 93.9 mm for the fossil),

and the ulna of an immature but virtually full-grown female from Mexico (RWD 12,023) measures 88.9. Ulnae of three males from Mexico range from 94.5 to 99.5 in length. The type humerus and ulna and Murray's referred complete ulna (UMMP V48914) are heavier than the ulnae of the two small Recent birds from southern California, which may be an indication that *A. elasson* was a stronger flier than Recent *Aechmophorus*. Murray also attributed the distal ends of two other ulnae to *A. elasson*. These, however, are not as heavy as those of the small southern California birds, but the lengths of these fossils cannot be determined so their relative proportions are unknown.

Two nearly complete coracoids (UMMP 49578 and 49582) and the proximal end of a tarsometatarsus (UMMP V52403) were referred by Murray to *Aechmophorus elasson*. These are smaller than those of the two small southern California birds. Also in the UMMP and referred to *A. elasson*, but not mentioned by Murray, are the distal end of a radius (UMMP 48904), the distal 94.7 mm of a tibiotarsus (UMMP 52545), and a cervical vertebra (UMMP 52527).

Recently, Chandler (1990) reported *Aechmophorus elasson* from Upper Pliocene deposits of the San Diego Formation. His referred material included one ulna, one femur, one tibiotarsus, and two tarsometatarsi. The only measurements presented were for a cast of the type and two other ulnae, which he compared with those of four Recent *A. occidentalis*, less than half the number used by Murray (1967).

Using the loons (Gaviiformes) and petrels (Procellariiformes) as outgroups, Chandler attempted to determine polarities for several skeletal characters of *Aechmophorus*, but neither gave reasons for his selection of these outgroups nor presented overall conclusions regarding the evolutionary relationships of *Aechmophorus*.

A careful comparison of all the available material attributed to *Aechmophorus elasson* with sufficient Recent material for adequate coverage of the range of geographic variation in the latter is badly needed.

PODILYMBUS

The genus *Podilymbus* consists of two Recent species: *P. podiceps* (Linnaeus 1758), which is widespread in North and South America, and *P. gigas* Griscom 1929, a probably flightless endemic on Lake Atitlán, Guatemala. The latter species is believed to have been derived from the former on Lake Atitlán, presumably as a crab-eating specialist (Zusi and Storer, 1969). It is therefore unlikely that it is of significance in identifying fossils from elsewhere.

The three subspecies of the Pied-billed Grebe differ in size. There is insufficient skeletal material from the South American race, *Podilymbus podiceps antarcticus* (Lesson 1842), or from the West Indies, *P. p. antillarum* Bangs 1913, for a statistical analysis, but data from study skins show that the former averages somewhat larger and the latter somewhat smaller than examples of the nominate race of continental North America (Table 1). No geographic variation has been verified within continental North America, and preliminary analysis of measurements of study skins from this area indicated that there is no significant change with latitude.

Fossils of *Podilymbus* were first reported by Shufeldt (1892) from Fossil Lake, Oregon, and referred to the Recent species. Later, Shufeldt (1913) described two tarsometatarsi and a coracoid from Fossil Lake as a new species, *P. magnus* Shufeldt 1913. This "species" has had a checkered history, having been recognized as a valid species, considered a temporal subspecies, or synonymized with *P. podiceps*. Its history is summarized in Storer (1976).

Analysis of a series (23 males and 15 females) of skeletons of Recent North American Pied-billed Grebes (Storer, 1976) showed that both of Shufeldt's tarsometatarsi of "*Podilymbus magnus*" are well within the range of the Recent form. Sexual dimorphism, as determined from means of this sample of tarsometatarsi is 10.5 percent for length and 12.2 percent for shaft width. Overlap between the sexes is slight, hence the sex of most fossil specimens can be assigned. The total range of measurements (sexes combined), expressed as percent of the mean, is 21 for length and 28.6 for shaft width. This is a large figure for a form without significant geographic variation.

After examining 220 fossil bones of *Podilymbus* from various Pleistocene localities in California, Florida, Nevada, and Oregon (including the type material of *P. magnus*) and comparing their measurements with those of 38 Recent North American piedbills, I concluded (Storer, 1976) that two tarsometatarsi and two femora from Florida, although similar in length to those of the Recent birds, had shafts too wide to be included in *P. podiceps*. (These widths were from 2.6 to 4.5 standard deviations above the means for the Recent sample.) These were described as a new species, *P. wetmorei* Storer 1976, and two humeri and one tibiotarsus were tentatively assigned to the new species. Campbell (1980:119) suggested that *P. wetmorei* might have been "a resident race of *P. podiceps* in peninsular Florida during the Pleistocene." This interpretation cannot be ruled out, although the greater relative thickness of the bones suggests a greater difference in proportions than that commonly found in different subspecies of grebes.

The only other fossil pied-bill is *Podilymbus majusculus* Murray 1967 from the Upper Pliocene Glenns Ferry Formation of Idaho. This grebe had a longer and relatively more slender tarsometatarsus and a shorter, heavier femur than the living form. This suggests that the fossil species was better adapted for pursuit diving in open water, whereas *P. podiceps* may be better adapted for breast-first "crash dives" and for foraging among emergent vegetation. If *P. majusculus* was ancestral to *P. podiceps*, a reversal in the general evolutionary trend in grebes for a long, narrow tarsometatarsus occurred in the evolution of this form.

PODICEPS

As Bickart (1990:11) has pointed out, the fossil species of grebes are in "great need of revision." This is particularly true of those of the genus *Podiceps*. Chandler (1990:89–95) has reported briefly on material from the Upper Pliocene San Diego Formation and described a new species, *Podiceps arndti* Chandler 1990, as slightly smaller than "*P. grisegena*" and differing in several characters of the leg bones. Unfortunately, he did not list the comparative material that he used. To my knowledge, no one has compared North American fossils of *Podiceps* with skeletons of the small nominate race of *P. grisegena* (Boddaert 1783) from Europe and western Asia. [The lengths of the humerus and tarsometatarsus of a small skeleton of *P. g. grisegena* from Europe are less than 75 percent of those of a large *P. g. holboellii* Rheinhardt 1853 from North America (Storer, unpubl. data).] While, on the surface, this may seem a trivial point, such a comparison could provide answers to questions regarding the evolutionary history of *P. grisegena*. At least two scenarios are possible. For example, did the species arise as a large form in North America, expand its range into Asia and Europe where the residents subsequently became smaller through competition with the larger *P. cristatus* (Linnaeus 1758)? Or did it arise as a

small species in Europe, expand its range eastward to North America where it became larger in the absence of *P. cristatus*? Analyses of adequate samples of both Recent forms are needed to interpret the size of the fossil species relative to the forms of *P. grisegena* and to determine the constancy of the other morphological differences between them. A detailed analysis of the increasing amount of fossil material available and of the abundant Recent material might well lead to an understanding of the evolutionary history of this and other Recent members of the genus.

Comparable studies of other groups of birds should also be made. One obvious choice would be a study of the cormorants and anhingas in the context of Siegel-Causey's (1988) analysis of the skeletal characters of Recent members of the group. Others would be the loons (Gaviidae) and the auks (Alcidae), for which large numbers of fossils have been collected.

CONCLUSIONS

First, size can only be used with confidence when the amount of variation within the same or related species is understood. Intraspecific differences can be based on sex, age, or geography, or they may be individual. For example, humerus length in our sample of six Pacific Loons, *Gavia pacifica* (Lawrence 1858), a species in which geographic variation has not been described, ranges from 130 to 168 mm, a difference amounting to 29 percent of the smaller measurement. Knowledge of the social systems of Recent species can be important in assessing size variation in fossils. Like those of most geese, family groups of the Canada Goose, *Branta canadensis* (Linnaeus 1758), move together between the breeding and wintering grounds and mate within their group. As a result of this restriction of mate choice, many subspecies have evolved and the range of size variation within this species is more than twice that in the Pacific Loons mentioned earlier. How far into the past such information can be useful is unknown, but it is certainly important in comparisons of Pleistocene and Recent material. Not only is size variable, but also proportions and the relative development of ossification around muscle scars can vary with age, more reasons why adequate series of Recent material are needed for thorough comparisons with fossil material.

We should keep in mind that there are, and presumably were in the past, sets of sibling species that cannot be distinguished on the basis of skeletal characters. Furthermore, there are pairs of very similar species with allopatric distribution in eastern and western North America. Identifying fossils of these on the basis of range, unless so stated, can result in errors in summaries of distributional data.

We have learned much about individual, sexual, and geographic variation within Recent species. We have not only an increasingly large number of fossils and people to study them, but also increasingly large numbers of skeletons of Recent birds for comparisons. [See the world inventory of this material by Wood and Schnell (1986).] We have also entered (some of us kicking and screaming) a computer age in which increasingly sophisticated methods of analysis can assist us in evaluating possible differences between fossil birds and their living counterparts. If we can utilize to best advantage all these assets, I think that the future of paleornithology will be bright.

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REGIONAL SURVEYS

ZOOGEOGRAPHY AND EVOLUTION OF THE AVIFAUNA OF THE CANARY ISLANDS

Marcos Báez

ABSTRACT. The taxonomy and zoogeographic characteristics of the Canary Islands avifauna are analyzed within the context of theories of island biogeography. Aspects studied include the existence of faunal turnover, the species–area relationship, the possible evidence of geographical relicts, the phenomenon of extinction, and the existence of fossils.

Key words: zoogeography, avifauna, Canary Islands, evolution.

INTRODUCTION

The avifauna of the Canary Islands has long been of interest to naturalists and biologists. The first contribution to our knowledge of this avifauna was from Andre-Pierre Ledru, as early as 1796 (Ledru, 1982). The most noteworthy subsequent works are those of Volsoe (1951, 1955) and Bannerman (1963). The works of Volsoe are particularly relevant as they consider the evolution and biogeography of the Canary Islands avifauna. The present work analyzes the biogeography and evolution of the avifauna of the Canary Islands from the viewpoint of the theory of island biogeography, and it comments on other aspects of the avifauna, such as the presence of relicts or the extinction of certain species. An updated checklist (Table 1) is presented of the breeding avian species and their distribution throughout the Canary Islands.

THE CANARY ISLANDS

The Canary Islands archipelago consists of seven primary volcanic islands situated between 27°–29°N and 13°–18°W (Fig. 1). The distance between the coast of the African continent and the closest island of the Canaries is about 90 km, and this distance is about 380 km for the islands farthest from Africa. The depth of the sea between the Canaries and the African continent is over 1,000 m, whereas the depth of the sea between some of the islands is over 2,000 m. Geologists currently maintain that the volcanic Canary Islands are of oceanic origin and assign ages that vary from 1 to 20 Ma (Abdel-Monem et al., 1971; Araña and Carracedo, 1979), each island being of a different age.

The climate is warm-temperate and, as a result of the strong oceanic influence, the mean temperatures are much below those on the adjacent African continent. On Lanzarote and Fuerteventura rainfall is ca. 140 mm/year, but increases westward to 585 mm/year on La Palma, one of the most remote of the western islands.

GENERAL AFFINITIES OF THE AVIFAUNA

The Palaearctic nature of the avifauna of the Canary Islands is clearly evident, in both the distribution of the species involved and their taxonomic affinities. Palaearctic elements comprise 68 percent of the total.

Although some of the species are widely distributed, i.e., Holarctic, Old World, etc., the Canarian populations belong either to subspecies that are typically North African, Iberian, or European, or to endemic subspecies with close affinities to corresponding subspecies present in the areas just mentioned. The same pattern of affinity is shared by the six endemic species of the archipelago, including two extinct species. The relationships of the endemic species are as follows.

Haematopus meadewaldoi Bannerman 1913: This species is presently considered to be extinct. It was relatively common during the first third of the nineteenth century, being observed in La Graciosa by Berthelot in 1829 (Berthelot, 1839), but it was already rare at the beginning of the twentieth century (Bannerman, 1963). It was considered a subspecies of the African Black Oystercatcher (*H. ostralegus* Linnaeus 1758) until Hockey (1982) raised it to specific status and referred to it as *H. meadewaldoi.*

Fringilla teydea Webb, Berthelot and Moquin-Tandon 1841: This species is considered to be closely related to the European species *F. coelebs* Linnaeus 1758. Azorian populations of *F. coelebs* tend to show convergent evolution with the Canarian *F. teydea* (Grant, 1979).

Columba junoniae Hartert 1916 and *Columba bollii* Godman 1872: These two laurel pigeons are endemic to the Canary Islands. *Columba bollii* is related to the Palaearctic species *C. palumbus* Linnaeus 1758 and *C. junoniae* is related to *C. oenas* Linnaeus 1758 (Volsoe, 1951). *Columba bollii* has been considered to be conspecific with *C. trocaz* Heineken 1829 of Madeira, but *C. bollii* is as close to *C. junoniae* as it is to *C. trocaz.* The three species would probably be considered to be a single su-

Table 1. Checklist of breeding avian species and their insular distribution. The islands are identified by the following: H, El Hierro; G, La Gomera; P, La Palma; T, Tnerife; C, Gran Canaria; F, Fuerteventura; L, Lanzarote.

	H	G	P	T	C	F	L
Bulweria bulwerii	+			+			+[1]
Calonectris diomedea borealis	+	+	+	+	+	+	+
*Puffinus puffinus**							
Puffinus assimilis baroli	+			+	+		
Hydrobates pelagicus	+			+			+[2]
Oceanodroma castro			+[3]				
*Ardea cinerea**							
Neophron percnopterus percnopterus				+	+	+	+
Accipiter nisus granti	+	+	+	+	+		
Buteo buteo insularum	+	+	+	+	+	+	+
Pandion haliaetus haliaetus	+	+		+		+	+
Falco tinnunculus canariensis	+	+	+	+	+		
Falco tinnunculus dacotiae						+	+
Falco pelegrinoides pelegrinoides					+	+	+
Falco eleonorae						+	+
Alectoris barbara koenigi		+		+		+	+
Alectoris rufa intercedens					+		
Coturnix coturnix confisa	+	+	+	+	+	+	+
Numida meleagris				+			
Gallinula chloropus chloropus				+	+	+	
Chlamydotis undulata fuerteventurae						+	+
Burhinus oedicnemus distinctus	+		+	+	+		
Burhinus oedicnemus insularum						+	+
Cursorius cursor cursor					+	+	+
Charadrius dubius curonicus				+	+	+	
Charadrius alexandrinus alexandrinus				+	+	+	+
Scolopax rusticola		+	+	+			
Larus argentatus atlantis	+	+	+	+	+	+	+
Sterna hirundo hirundo	+	+	+	+		+	
Columba livia livia	+	+	+	+	+	+	+
Columba bollii	?	+	+	+			
Columba junoniae		+	+	+			
Streptopelia turtur turtur	+	+	+	+	+	+	+
Pterocles orientalis orientalis						+	
Tyto alba alba	+			+	+		
Tyto alba gracilirostris						+	+
Asio otus canariensis	+	+	+	+	+		
Apus unicolor	+	+	+	+	+	+	+
Apus pallidus brehmorum	?	?	?	+	+	+	+
Upupa epops epops	+	+	+	+	+	+	+
Dendrocopos major canariensis				+			
Dendrocopos major thanneri					+		
Calandrella rufescens rufescens				+			
Calandrella rufescens polatzeki					+	+	+
Anthus berthelotii berthelotii	+	+	+	+	+	+	+
Motacilla cinerea canariensis		+	+	+	+		
Erithacus rubecula superbus				+	+		
Erithacus rubecula rubecula	+	+	+				
Turdus merula cabrerae	+	+	+	+	+		

Table 1. Continued.

	H	G	P	T	C	F	L
Sylvia conspicillata orbitalis	+	+	+	+	+	+	+
Sylvia melanocephala leucogastra	+	+	+	+	+	+	+
Sylvia atricapilla heineken	+	+	+	+	+		
Phylloscopus collybita canariensis	+	+	+	+	+		
Regulus regulus teneriffae	+	+	+	+			
Parus caeruleus teneriffae		+		+	+		
Parus caeruleus ombriosus	+						
Parus caeruleus palmensis			+				
Parus caeruleus degener						+	+
Lanius excubitor koenigi				+	+	+	+
Corvus corax tingitanus	+	+	+	+	+	+	+
Pyrrhocorax pyrrhocorax barbarus			+				
Sturnus vulgaris vulgaris				+	+		
Passer hispaniolensis hispaniolensis	+	+	+	+	+	+	+
Petronia petronia madeirensis	+	+	+	+	+		
Fringilla coelebs tintillon		+		+	+		
Fringilla coelebs ombriosa	+						
Fringilla coelebs palmae			+				
Fringilla teydea teydea				+			
Fringila teydea polatzeki					+		
Serinus serinus				+	+		
Serinus canaria	+	+	+	+	+		
Carduelis chloris aurantiiventris				+	+		
Carduelis carduelis parva	+	+	+	+	+	+	+
Carduelis cannabina meadewaldoi	+	+	+	+	+		
Carduelis cannabina harterti						+	+
Bucanetes githagineus amantum		+		+	+	+	+
Miliaria calandra calandra	+	+	+	+	+	+	+
Saxicola dacotiae dacotiae						+	
Saxicola dacotiae murielae							+[4]

[1] El Hierro records are from Roques de Salmor. Lanzarote records are from the small island of Montaña Clara.

[2] These records are from small islands around El Hierro, Tenerife and Lanzarote, respectively.

[3] This record is from Roques de Anaga, close to the north coast of Tenerife.

[4] This subspecies is found only on the small islands of Montaña Clara and Alegranza, close to Lanzarote.

* Reproduction not confirmed.

perspecies were it not for the complete geographical overlap of *C. bollii* and *C. junoniae* (Cramp, 1985).

Carduelis triasi Alcover and Florit 1987: This is an extinct species recorded from the island of La Palma; it was closely related to the European species *C. chloris* (Linnaeus 1758). It is presumed to have become extinct sometime during the last two centuries (Alcover and Florit, 1987).

Saxicola dacotiae (Meade-Waldo 1889): This species is so similar to the Palaearctic species *S. torquata* Linnaeus 1766 that it was considered to be conspecific by Volsoe (1951). Never-

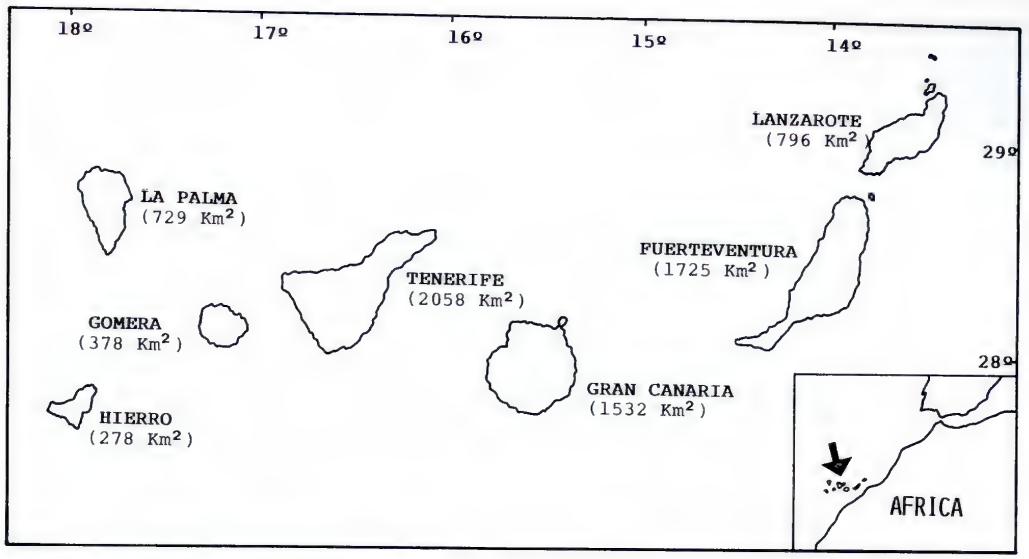

Figure 1. Map of Canary Islands, with area for each island.

theless, its status as a valid species is now established (Collar and Stuart, 1985).

In addition to these Canarian endemics, the species *Anthus berthelotii* Bolle 1862, *Apus unicolor* (Jardine 1830), and *Serinus canaria* (Linnaeus 1758) are Macaronesian endemics. The first two species are found in Madeira and the Canaries, whereas the third is found in the Azores, Madeira, and the Canaries. *Anthus berthelotii* and *S. canaria* are considered closely related to the European species *A. campestris* (Linnaeus 1758) and *S. serinus* Linnaeus 1766, respectively, and may indeed be members of respective superspecies (Moreau, 1966). Such relationships assume that the colonization of the Canaries has proceeded from North Africa or southern Europe, in many cases through Madeira. The possibility of colonization from the Azores has also been suggested (Grant, 1980).

FAUNAL TURNOVER

Some 63 species of birds, four of which are Canarian endemics and three of which are Macaronesian endemics, breed in the Canary Islands at the present time. One group of 26 nonendemic species are represented by 26 Canarian endemic subspecies and 10 Macaronesian endemic subspecies. Another group of 30 nonendemic species do not have taxonomically differentiated populations on the islands.

Following Darlington (1971), if it is assumed that endemic subspecies have been on the islands for a longer time than nonendemic forms and endemic species on the islands even longer, one can pursue the following analysis of the Canarian avifauna.

Approximately one-half of the birds that breed in the islands have not obviously differentiated from the continental populations from which they originated. Therefore, their colonization is presumed to be recent since a time span of less than 10,000 years may be sufficient for isolated populations to undergo evolutionary changes (Bock, 1979). About 43 percent of the avifauna is subspecifically differentiated from continental populations. It can be assumed that their arrival may have taken place within the last 50,000 years, since this time span might be sufficient for such a differentiation (Fleming, 1962; Campbell, 1979).

The arrival of populations presently differentiated as endemic species could have occurred as late as the early to middle Pleistocene, since a million years is sufficient time in which to attain specific differentiation (Fleming, 1962). These endemics represent only 6.5 percent of the avifauna (10 percent if the two extinct species are included), and this percentage is notably lower than that for endemism in other faunistic groups of the Canary Islands: ca. 100 percent in reptiles, ca. 80 percent in Dermaptera, ca. 70 percent in Trichoptera, ca. 40 percent in Diptera, and ca. 26 percent in Heteroptera (Báez, 1982). If one takes into account that the ages of the islands vary from 1 to 20 million years, such a low level of differentiation within the avifauna is difficult to explain. Therefore, the avifauna must have undergone faunal turnover, with a continuous cycle of colonization–extinction similar to what is presumed to have occurred in older, more isolated archipelagos, such as New Caledonia or New Zealand (Mayr, 1965). This assumes that the endemic species and subspecies are the result of evolutionary differentiation. The possibility that some endemics may represent geographical relicts is discussed below.

THE SPECIES–AREA RELATIONS

One of the features of islands is that they have rather few species on them. But what are the variables that determine the number of species on islands? The conclusions reached in several studies of the subject (see Williamson, 1981, for a discussion) coincide greatly in that the island's area is always considered important, its altitude is occasionally important and its distance from the mainland is seldom important.

Data on the number of landbird species, area and altitude of the islands, and the diversity of the vegetation are given in Table 2. Multiple regression of the number of landbird species (dependent variable) against log area, log altitude, and "vegetation diversity" (Humphries, 1979), all independent variables, indicates that log area and log altitude together have a significant multiple correlation with the number of landbirds (Table 3). The inclusion of "vegetation diversity" results in an insignificant multiple regression, thereby indicating that it does not contribute to the prediction of avian diversity in this study.

The species–area relationship generally conforms to the pow-

Table 2. Data on the number of species, area, altitude, and "vegetation diversity."

Islands	Number landbirds	Area (km^2)	Altitude (m)	"Vegetation diversity"*
Tenerife	48	2,058	3,717	6
Gran Canaria	43	1,534	1,949	4
La Gomera	33	378	1,487	3
Fuerteventura	33	1,731	807	1
La Palma	32	728	2,426	5
El Hierro	29	277	1,500	4
Lanzarote	29	796	670	1

* After Humphries (1979).

Table 3. Stepwise multiple regression analysis between the number of landbird species (the dependent variable) and log area, log altitude, and "vegetation diversity" (the independent variables).

Variables	R^2	F	P
Log area	0.50	5.01	0.07
Log area + log altitude	0.84	10.69	0.02
Log area + log altitude + vegetation diversity	0.86	5.96	0.08

er function model: $S = cA^z$. The value of z has been the subject of many studies. Preston (1962) suggests that the values of z vary between 0.17 and 0.33, whereas May (1975) extends these limits to 0.15–0.39. MacArthur and Wilson (1967) suggested that the limits of z are to be found between 0.20 and 0.35, whereas Connor and McCoy (1979) suggest limits of 0.20–0.40. Within these limits, the values of z are lower in continental areas ($0.12 < z < 0.17$; MacArthur and Wilson, 1967) than in those archipelagos whose biota is found to be in equilibrium ($0.20 < z < 0.35$; MacArthur and Wilson, 1967) and attain the highest values ($z > 0.35$) in those archipelagos where extinction rates have been higher than immigration rates (Brown, 1978).

In the case of the landbirds of the Canary Islands, the value of z is very low ($z = 0.17$), below the limit of 0.20 predicted by Preston (1962) for the slope of the log/log model for true isolates. It is also lower than the index obtained for birds of other archipelagos: West Indies ($z = 0.237$), East Indies ($z = 0.280$), and east-central Pacific ($z = 0.303$) (Hamilton et al., 1964). The index is similar to that obtained for the birds of the Galápagos ($z = 0.17$; Harris, 1973) and for the lizards of the California Channel Islands ($z = 0.166$; Case, 1975). The reason for the low value of z for the landbirds of the Canary Islands may be their proximity to the African continent, because slopes tend to be low for archipelagos that are close to the mainland and high for isolated archipelagos (MacArthur and Wilson, 1967).

A different point of view is that upheld by Steadman (1986), who does not accept the species–area equation and other aspects of the equilibrium theory of island biogeography. His main objection is that the theory does not take into account "the prehistoric and historic factors that have influenced insular biotas" (Steadman, 1986:79), an argument that may help explain the biogeographical characteristics of the landbird fauna of the Canary Islands. Although very few fossils of birds have been found in these islands (see later), this is probably a consequence of a lack of research. For example, several species of fossil birds have been found on the neighboring island of Madeira in recent years (Pieper, 1985). Prehistoric and historic factors undoubtedly affect the application of the theory of island biogeography and should always be considered in island avifaunal analysis.

INSULAR DIFFERENTIATION OR GEOGRAPHICAL RELICTS?

The Canary Islands avifauna may be analyzed from two totally different points of view. The endemic forms, species and subspecies, may be considered to be a result of evolutionary divergence, or they may be considered to be relicts of continental forms that became extinct because of the climatic changes that occurred during the Pleistocene.

For example, Lack (1969) gives the following list for the percentage of the total avifauna that are represented by endemic subspecies in the northeast Atlantic islands: Ireland, 3; Iceland, 21; Azores, 30; and Canaries, 45. His purpose was to demostrate that isolation, i.e., distance from the island or archipelago to continental zones, is not the main factor influencing the degree of endemism. However, these different percentages could also be the result of the variation of climate with latitude in the Pleistocene. The most northerly situated islands would be colonized later than the more southerly ones, such that the time available for evolutionary divergence to take place has been longer for the more southerly archipelagos.

Islands are ideally suited to species diversification, a fact that is well known and frequently stated in reports and textbooks. Nevertheless, there is the possibility that a part of the avifauna of the Canaries may be a relict, as is thought to be the case in Canarian *Drosophila subobscura* (*Diptera, Drosophilidae*) (Prevosti, 1974). And, for example, the Macaronesian endemic pipit, *Anthus bertheloti* is considered by Volsoe (1951, 1955) to be a primitive form related to *A. campestris*, the plesiomorphic character being the streaked plumage. Does *A. bertheloti*, therefore, represent a geographical relict in the Macaronesian avifauna?

Some of the endemic subspecies have also been considered to be primitive forms. Thus, Voous (1947) proposed that the subspecies of Canarian woodpecker, *Dendrocopos major* (Linnaeus 1758), are remnants of the European populations of the Mindel/Riss Interglacial, compelled by the Riss Glaciation to take refuge to the east and west of the Mediterranean region. Johansen (1947) considers the Canarian population of *Phylloscopus collybita* (Vieillot 1817) to be the most primitive of all the subspecies of this species and also to be the survivor in insular refugia of the populations of Europe during the last interglacial period. The same reasoning is employed by Volsoe (1951) when he considers the western Canarian subspecies of *Parus caeruleus* Linnaeus 1758 and the subspecies *Erithacus rubecula superbus* Köenig 1889 to be primitive forms. Löhr and Thaler (1980) also regard the Canarian populations of *Regulus regulus teneriffae* Seebohm 1883 as representing a primitive form with specific rank.

Finally, among the endemic species of birds in the Canary Islands the two laurel pigeons have been considered by Volsoe (1951) to be relict populations of the ancestors of the European Ring Dove (*Columba palumbus*) and Stock Dove (*Columba oenas*), respectively, rather than having diverged directly from a colonization of these mainland species.

However, all of these interpretations regarding relictual components of the Canarian avifauna must be treated with some scepticism because they are not based on thorough phylogenetic analyses of the species involved.

EXTINCTIONS

The possibility of extinction of insular populations is much greater than in continental populations (MacArthur and Wilson, 1967) because the former are generally represented by small populations that are restricted to a few habitats. According to Mayr (1965), extinctions on islands are more frequent than generally believed and they are not necessarily caused by competition, as suggested by MacArthur and Wilson (1967), but rather by climatic fluctuations of biotic changes of any kind. On the other hand, Olson and James (1982) and Steadman (1986) stress the importance of the modifications of the environment by man in cases of massive extinctions in islands.

It is assumed that extinctions of several species of birds have taken place in the Canary Islands, but only four examples of extinct birds are known: two shearwaters, *Puffinus holei* Walker, Wrag and Harrison 1990 and *P. olsoni* McMinn, Jaume and Alcover 1990; a Cardueline finch (*Carduelis triasi* Alcover and Florit 1987; and remains of large fossil eggs attributed to ratites (Sauer and Rothe, 1972). However, additional remains of fossil birds of unidentified species have been found (Alcover and Florit, 1987), which is to be expected considering the large number of fossil bird species found on other islands or archipelagos; e.g., St. Helena (Olson, 1975), Hawaii (Olson and James, 1982), Bahamas (Olson, 1982), Galápagos (Steadman, 1986), Madeira (Pieper, 1985).

The small proportion of endemics in the Canary Islands avifauna argues for a substantial rate of extinction if one accepts Diamond's (1984) proposition that the percentage of endemics in an insular biota is inversely proportional to the rate of extinction. It is possible that the proximity of the Canaries to Africa enhances immigration, which in turn increases the number of synchronous species and, consequently, the rate of extinction.

Carduelis triasi was recently reported as a Holocene species by Alcover and Florit (1987) from a lava tube in the island of La Palma. *Carduelis triasi* is closely related to the European species, *C. chloris*, although it was larger with a smaller wing surface. *Carduelis chloris* is a recent immigrant to the Canaries and can be considered to have colonized the islands of Gran Canaria and Tenerife between 1967 and 1970 (Martin, 1987). Alcover and Florit (1987) speculated as to whether *C. triasi* and *C. chloris* may have shared a common ancestor or *C. triasi* became differentiated from an older immigration of *C. chloris*. A solution to this problem can only be provided by new data.

Alcover and Florit (1987) also suggest the possibility that the Carduelinae may have undergone an evolutionary radiation in the Macaronesian archipelagos similar to that undergone by the Carduelinae in Hawaii and the Emberizidae in the Galápagos. There are two reasons to question this view. First, it is possible that "endemic species" in the Canaries (both living and extinct) may, in reality, represent geographic relicts of continental species. Second, the evolutionary radiations of the Carduelinae in Hawaii and the Emberizidae in the Galápagos do not have any equivalents in the Africa islands (Moreau, 1966).

The other definitive extinction event in the Canaries is represented by the discovery on the island of Lanzarote of remains of large fossil eggs from the Miocene or Pliocene that have been identified as those of ostriches and aepyornithids (Sauer and Rothe, 1972). There are, however, doubts about the identity of these eggs. Many authors consider ratites to be a monophyletic group (Cracaft, 1974; Prager et al., 1976; Sibley and Ahlquist, 1981), which implies that the group originated in Gondwanaland prior to the separation of southern continents (130–100 Ma). Because ratites cannot fly, their presence on Lanzarote would imply that this island once formed part of the African continent (Sauer and Rothe, 1972; Rona and Nalwak, 1970; Dietz and Sproll, 1970), an opinion shared by others who have worked with the phylogeny of ratites (Cracaft, 1973; Sibley and Ahlquist, 1981). However, if Lanzarote has never formed a part of the African continent (Abdel-Monem et al., 1971; Araña and Carracedo, 1979), and these birds were indeed ratites, they must have arrived by some others means, such as rafting on vegetation (Báez, 1982).

It is possible that the eggs were not produced by ratites. Sauer and Rothe (1972) considered that there were two types of eggshell, which they attributed to either ostriches or aepyornithids on the basis of their porosity. However, porosity may not be a reliable method of identification because regardless of the species to which they belong, the larger a bird's egg, the greater the size of the pores and the lower their density (number pores/cm^2) (Tullet and Board, 1977). Báez (1982) suggested that the large birds that inhabit Lanzarote may have been descendents of winged ancestors that arrived on the island by their own means. Olson (1973) and Olson and James (1982) suggested that the loss of capacity to fly in insular birds is a rapid process. It may not require more than 1.5–1.8 million years, as non-flying birds are known from islands of this geological age. James and Olson (1983) suggest that the loss of flight is typically a neotenic process brought about by the selective pressures of the absence of predators and the saving of energy.

The geological age of Lanzarote, 11–20 million years (Araña and Carracedo, 1979), is more than sufficient for this process to have taken place. This would explain the presence of these large birds without having to resort to hypothetical land bridges (Sauer and Rothe, 1972) or to passive transport (Báez, 1982, 1987). Bones of these birds must be found before any conclusions regarding the origins of the eggs can be reached.

Finally, another aspect of the extinction of the avifauna in the Canary Islands is the presence of flowering plants that are typically fed upon by nectivorous birds. These are *Canarina canariensis* (L.) Vatke 1874 (*Campanulaceae*), *Isoplexis canariensis* (L.) Loud 1829 (*Scrophulariaceae*), *Isoplexis isabelliana* (Webb and Berthelot) Masferrer 1882, and *Lotus bertheloti* Masferrer 1881 (*Fabaceae*) (Olesen, 1985). These plants are occasionally visited by opportunistic species such as *Sylvia melanocephala* (Gmelin 1789), *Sylvia conspicillata* Temminck 1820, and *Phylloscopus collybita* (Olesen, 1985), but their presence may be evidence of an earlier presence of nectivores in the Canary Islands. The East African members of *Canarina* Linnaeus 1771 are certainly pollinated by birds (Ehrendorfer, 1979). Vogel (1954), following this logic, postulated the previous occurrence of Nectariniidae in Macaronesia.

The existence of Canarian Nectariniidae is perfectly feasible if we accept that their current distribution is sub-Saharan Africa and Madagascar represents a contraction of a wider Pleistocene distribution (Darlington, 1957). The presence of a species of sunbirds in Sokotra (Moreau, 1966) and the botanical affinities of relict groups between that island and the Canaries (Bramwell, 1976) also suggests that the Nectariniidae may previously have had a wider distribution.

HUMAN ACTIONS

Historic extinctions of the avifauna in the Canaries appear to have been caused directly by human actions, as in the case of *Haematopus meadewaldoi* and *Milvus milvus* (Linnaeus 1758) (Martin, 1987). It is possible that the prehistoric disappearance

of *Carduelis triasi* is also because of human activity (Alcover and Florit, 1987).

The extinctions of local, i.e., insular, populations have taken place because of the destruction of the natural habitat of the species in question. For example, in Gran Canaria man completly destroyed the laurel forests and the typical pigeons of these forest have disappeared, being last sighted toward the end of the last century (Tristam, 1889). The species *Neophron percnopterus* (Linnaeus 1758) has also disappeared from the island of La Gomera in the last 30 years, and it is at present nearing extinction on the islands of Tenerife and Gran Canaria (Martin, 1987). This is a consequence of the decrease in the number of carcasses of domestic mammals, currently their main source of food.

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THE PRESENT STATE OF KNOWLEDGE OF THE TERTIARY BIRDS OF CENTRAL EUROPE

Jiří Mlíkovský

ABSTRACT. Tertiary birds are recorded from 132 localities of Central Europe that range in age from the Late Paleocene to the latest Pliocene. The Early and Middle Miocene localities have furnished particularly significant numbers of fossil birds. Most of the birds collected have not yet been described, and many of those described are often in need of revision. At least 88 species and subspecies of Tertiary birds (excepting *nomina nuda*, but including two alleged bird species) are based on fossil material originating from Central Europe. Approximately 54 percent of these taxa were not listed in Brodkorb's (1963, 1964, 1967, 1971, 1978) *Catalogue of Fossil Birds*.

New taxonomic conclusions are as follows: (1) *Cygnus csakvarensis* belongs in the genus *Olor;* (2) *Anas isarensis* is an indeterminate member of the tribe Aythyini; (3) *Anas atava* belongs in the genus *Cygnus;* (4) *Anas eppelsheimensis* is Anseridae *incertae sedis;* (5) *Athene noctua veta* is synonymous with the modern *Aegolius funereus;* (6) *Ardea lignitum* is synonymous with the modern *Bubo bubo;* and (7) *Eleutherornis helveticus, Anas risgoviensis, Anas meyerii, Gallus longaevus, Totanus praecursor, Scolopax baranensis, Gallinago veterior,* and *Turdoides borealis* should be considered Aves *incertae sedis* until their types are restudied.

ZUSAMMENFASSUNG. Die tertiären Vögel wurden bisher in 122 Lokalitäten Mitteleuropas gefunden, die über den Zeitraum vom späten Paläozän bis zum jüngsten Pliozän verbreitet sind. Davon haben insbesondere früh- und mittelmiozäne Fundstellen bedeutende Mengen von Vögelknochen geliefert. Leider sind dir meisten del gesammelten Vögel noch nicht beschrieben worden und diejenigen, deren Beschreibungen bereits publiziert worden sind, brauchen in vielen Fällen eine Revision. Wenigstens 88 Arten und Unterarten von tertiären Vögeln (ausschliesslich von *Nomina nuda*, aber einschliesslich von 2 Arten angeblicher Vögel) wurden auf dem aus Mitteleuropa stammenden Material begründet. Ungefähr 54 prozentig davon wurde im Brodkorb's (1963, 1964, 1967, 1971, 1978) *Catalogue of Fossil Birds* nicht registriert.

Folgende taxonomische Schlussfolgerungen sind neu: (1) *Cygnus csakvarensis* gehört der Gattung *Olor* an; (2) *Anas isarensis* ist ein nicht näher unbestimbares Vertreter des Tribus Aythyini; (3) *Anas atava* gehört der Gattung *Cygnus* an; (4) *Anas eppelsheimensis* ist ein Anseridae *incertae sedis;* (5) *Athene noctua veta* ist mit dem rezenten *Aegolius funereus* synonym; (6) *Ardea lignitum* ist mit dem rezenten *Bubo bubo* synonym; und (7) *Eleutherornis helveticus, Anas risgoviensis, Anas meyerii, Gallus longaevus, Totanus praecursor, Scolopax baranensis, Gallinago veterior,* and *Turdoides borealis* sind, solange ihre Typen nicht revidiert werden, als Aves *incertae sedis* zu betrachten.

Key words: Aves, Tertiary, Central Europe.

INTRODUCTION

The fossil record of birds is often considered too incomplete to be useful in phylogenetic, stratigraphic, or faunal studies. A recent review by Olson (1985) showed that much information is contained in the avian fossil record, but highlighted the necessity to reevaluate the results of those workers who based their taxonomic determinations and/or descriptions of fossil birds on inadequate materials, or whose work was subject to other potential kinds of errors.

Reviews of previous studies of fossil birds may be pursued either by taxon or by region. Whereas the former approach allows more insight into the evolution of the taxon under study, the latter makes it possible to recover local publications on the topic and to be more up-to-date with local geographic and stratigraphic data. The present paper aims to contribute to the latter kind of work by summarizing our present knowledge of the Tertiary birds of Central Europe, which is defined for the purposes of this paper as an area including Germany, Poland, Czechoslovakia, Hungary, Austria, Liechtenstein, and Switzerland (Fig. 1). The area covers approximately 1,015,632 km^2.

HISTORY OF TERTIARY AVIAN RESEARCH IN CENTRAL EUROPE

Bird remains from Tertiary deposits of Central Europe were first mentioned by Swiss naturalist Johann Jacob Scheuchzer (1670–1733), who described an "ante-diluvian" (=Middle Miocene) feather from Öhningen, Germany (Scheuchzer, 1708). Regular research was started much later, around the middle of the nineteenth century, by German paleontologist Hermann von Meyer (1801–1869). Meyer (1844) also formally named the first Tertiary bird species of Central Europe, *Protornis glarniensis* from the Lower Oligocene of Matt, Switzerland. During the remainder of the nineteenth and early twentieth centuries, no workers were regularly studying Tertiary birds of Central Europe. Those that were, were only marginally interested in fossil birds, such as Oskar Fraas (1824–1897), Gustav Carl Laube (1839–1923), and Ludwig von Ammon (1850–1922), all of whom produced paleornithological works of generally low quality.

The classical period of Central European paleornithology culminated with the Hungarian paleornithologist Kálmán Lam-

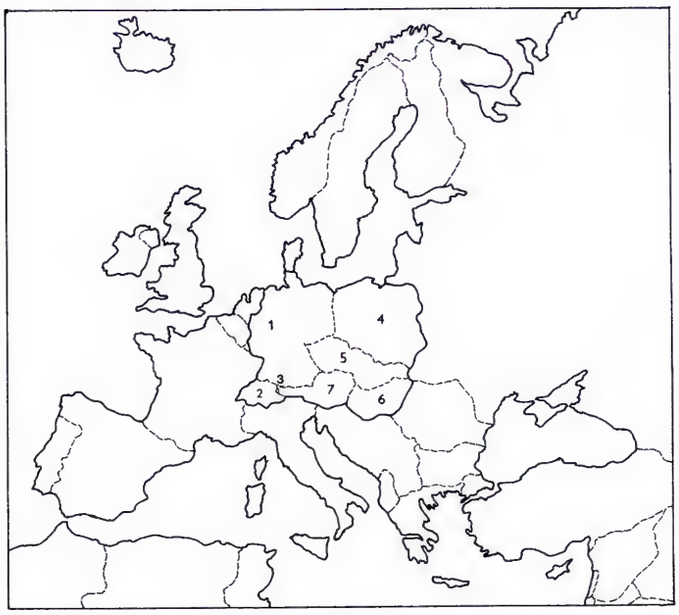

Figure 1. Map of Europe, indicating the area of Central Europe covered in the present paper. **1,** Germany; **2,** Switzerland; **3,** Liechtenstein; **4,** Poland; **5,** Czechoslovakia; **6,** Hungary; **7,** Austria.

brecht (1889–1936), who described fossil birds from such Tertiary localities of Central Europe as Geisel Valley, Ipolytarnóc, and Aumeister or Eppelsheim (see later) and presented the first comprehensive review of these birds (Lambrecht, 1933). Following his death, a hiatus appeared in Central European paleornithology that lasted until the late 1960s. Thereafter, research revived slowly and is at present carried out by Peter Ballmann, Dieter Stefan Peters, Angelika Hesse, and Karl-heinz Fischer in Germany, Zygmunt Bocheński in Poland, and Dénes Jánossy in Hungary. Several other workers of Central Europe intensively study Quaternary birds but have yet to contribute significantly to the study of the Tertiary birds of the region.

METHODS

I list all avian species and subspecies based on materials recovered from the Tertiary of Central Europe of which I am aware. The sequence of families follows, as far as possible, Wetmore (1960) for the sake of clarity, although considerable disagreement currently exists among avian systematists about this last standard offshoot of the classical Fürbringer–Gadow–Wetmore clade of avian classifiations (Wolters, 1975–1982; Cracraft, 1981; Mlíkovský, 1985; Olson, 1985). To facilitate the reader's orientation, I list all of the species in the systematic position that they occupied in the last catalogue of fossil birds (Brodkorb, 1963, 1964, 1967, 1971, 1978), if they were included in it, with only a few exceptions. I also follow this order because the taxonomic fate of many taxa is still unclear. For every species or subspecies, data on their original description, holotypes, and their location (if known) and on their age and locality from which they were described are given. Where appropriate, remarks are added. Figures in parentheses after each locality name refer to their numbers in the following section. [Localities with a letter added to their identifying number were added at press time; they are not included in the figures.—Ed.] Anatomical nomenclature follows Baumel et al. (1979) throughout the present paper.

Four species frequently listed among the Tertiary birds of Central Europe are not included here: (1) *Plotus pannonicus* Lambrecht 1916 was described from Tataros, a locality that was formerly in Hungary, but now lies in Rumania and is thus outside the region of concern; (2, 3) *Pliogallus crassipes* Gaillard 1939 and *Pliogallus kormosi* Gaillard 1939, formerly thought to be Pliocene phasianids of Hungary, were found to be based upon remains of Recent domestic hen (Jánossy, 1976a, 1976b); and (4) *Odontopteryx longirostris* Spulski 1910 was based upon a skull of unknown origin. Although it could have come from the Tertiary of Hamburg, northern Germany, as sometimes believed, this remains unproven (Olson, 1985:198) and the state of preservation of bones of the Tertiary birds of northern Germany and Denmark (Hoch, 1973, 1975) makes this improbable.

In addition, *Ornitholithes ralli* Anonymous is an etiquette name given for what was thought to represent a bird from the Middle Miocene of Öhningen, Germany (Karg, 1805:26), but which turned out to be a forgery (Pfannenstiel, 1958:854, fig. 1).

For stratigraphic divisioning of the Central European Tertiary, I follow Russell et al. (1982) for the Paleogene and Steininger et al. (1987) for the Neogene. Mammal Neogene units (*sensu* Steininger et al., 1987) are abbreviated as MN. It is recognized that the age of some localities is known only approximately and that disagreement still prevails among European stratigraphers as to the limits of many stratigraphic units. Consequently, the allocation of individual localities to specific stratigraphic units may be subject to future change.

Abbreviations used throughout are as follows.

BMNH:	Natural History Museum, London, United Kingdom; formerly British Museum (Natural History)
BSP:	Bayerische Staatssammlung für Paläontologie und historische Geologie, München, Germany
CHI:	Conservation Hall, Ipolytarnóc, Hungary
DP FNSP:	Department of Paleontology, Faculty of Natural Sciences, Charles University, Praha, Czechoslovakia
GIB:	Geological Institute, Budapest, Hungary
GIH:	Geologisches Institut, Hamburg, Germany
GM:	Geiseltalmuseum, Halle (Saale), Germany
GPIW:	Geologisch-Paläontologisches Institut der Universität, Würzburg, Germany
IZK:	Institute of Systematic and Experimental Zoology, Polish Academy of Sciences, Kraków, Poland
KD:	Mrs. Kessler, private collection, Darmstadt, Germany
MB:	Museum für Naturkunde, Humboldt-Universität, Berlin, Germany
MR:	Naturkundemuseum Ostbayern, Regensburg, Germany
MZ:	Paläontologisches Museum der Universität, Zürich, Switzerland
NFS:	Naturmuseum und Forschungsinstitut Senckenberg, Frankfurt (Main), Germany
NHMB:	Naturhistorisches Museum, Basel, Switzerland
NMB:	National Museum, Budapest, Hungary
NMP:	National Museum, Praha, Czechoslovakia
NMW:	Naturhistorisches Museum, Wien, Austria
RMT:	Regional Museum, Teplice, Czechoslovakia
SMNS:	Staatliches Museum für Naturkunde, Stuttgart, Germany

UM: Dr. U. Maschwitz, private collection, München, Germany
ZGIB: Zentrales Geologisches Institut, Berlin, Germany

SYSTEMATICS

Class Aves Linnaeus 1758

Subclass Ornithurae Haeckel 1866

Infraclass Ratitae Merrem 1813

Order Struthioniformes (Latham 1790)

Family Palaeotididae Houde and Haubold 1987

Palaeotis weigelti Lambrecht 1928

Palaeotis weigelti Lambrecht, 1928:20, text-fig. 6; pl. 1, figs. 1–4.

HOLOTYPE. Distal end of left tarsometatarsus with associated phalanx 1 digiti II; GM Ce I/4415 and Ce I/4418 (Haubold and Krumbiegel, 1984).

HORIZON AND LOCALITY. Middle Eocene of Geisel Valley (5).

REMARKS. When I studied the Geisel Valley bird fossils in 1983, I found that what was exhibited in the museum as the type of *Palaeotis weigelti* was, in fact, another specimen. The specimen on exhibit was a crushed partial skeleton, GM 4362, first mentioned in the literature probably by Weigelt (1942:30). The time of, and the reasons for, this substitution were unknown (H. Haubold, pers. comm., 1983).

Palaeotis weigelti was a flightless paleognathous bird (Houde and Haubold, 1987; Peters, 1988).

Palaeogrus geiseltalensis Lambrecht 1935

Palaeogrus geiseltalensis Lambrecht, 1935:361, pl. 1, fig. 1.
Ornitocnemus geiseltalensis: Brodkorb, 1967:148 (new combination).

HOLOTYPE. Associated right tibiotarsus, right tarsometatarsus, and two basal phalanges digitorum pedis; GM 5882. The phalanges were not described or figured by Lambrecht (1935).

HORIZON AND LOCALITY. Middle Eocene of Geisel Valley (5).

REMARKS. This species is synonymous with *Palaeotis weigelti* Lambrecht (1928) from the same horizon and locality (Houde and Haubold, 1987).

Family Struthionidae Vigors 1825

Struthio pannonicus Kretzoi 1954

Struthio (*Pachystruthio*) *pannonicus* Kretzoi, 1954:232, pls. 1, 2.

HOLOTYPE. Left pedal phalanx 1 digiti III; GIB, uncatalogued.

HORIZON AND LOCALITY. Upper Pliocene (MN 17) of Kisláng (114).

REMARKS. Kretzoi (1955) described additional material of this species. Mikhailov (1988) and Mikhailov and Kurochkin (1988) restudied associated eggshells and subsequently synonymized *Struthio pannonicus* with *Struthiolithus* (=*Struthio*) *chersonensis* Brandt 1873.

Infraclass Carinatae Merrem 1813

Order Gaviiformes Wetmore and Miller 1926

Family Gaviidae Allen 1897

Gavia egeriana Švec 1982

Gavia egeriana Švec, 1982:251, text-fig. 8a, pl. I, fig. 1a, b.

HOLOTYPE. Distal end of left humerus; DP FNSP 4816.

HORIZON AND LOCALITY. Lower Miocene (MN 4) of Dolnice 2 (67).

REMARKS. Additional finds from the same horizon and locality have been reported by Švec (1985).

Order Podicipediformes Fürbringer 1888

Family Podicipedidae Bonaparte 1831

Miobaptus walteri Švec 1982

Miobaptus walteri Švec, 1982:246, text-fig. 1a, b, pl. I, fig. 2.

HOLOTYPE. Proximal end of right humerus; DP FNSP 4810.

HORIZON AND LOCALITY. Lower Miocene (MN 4) of Dolnice 2 (67).

REMARKS. *Miobaptus walteri* is closely related to grebes of the modern genus *Tachybaptus* Reichenbach 1852 (Švec, 1982, 1984). As comparisons were made with only one species of the latter, *Tachybaptus ruficollis* (Pallas 1764), it is possible that the slight differences noted between *Tachybaptus* and *Miobaptus* are only a result of intrageneric variability.

Order Procellariiformes Fürbringer 1888

Family Diomedeoididae Fischer 1985

Diomedeoides minimus Fischer 1985

Diomedeoides minimus Fischer, 1985:114, figs. 1–6, 12, 13, 15, 16.

HOLOTYPE. Right humerus; MB Av. 764.

HORIZON AND LOCALITY. Middle Oligocene of Espenhain (21).

Order Pelecaniformes Sharpe 1891

Family Pelecanidae Vigors 1825

Pelecanus intermedius Fraas 1870

Pelecanus intermedius Fraas, 1870:281, pl. 13, figs. 3, 4.
Miopelecanus intermedius: Cheneval, 1984:77 (new combination).

HOLOTYPE. Skull with associated partial mandible; SMNS, uncatalogued.

HORIZON AND LOCALITY. Middle Miocene (MN 6) of Hahnenberg, Nördlinger Ries (82).

REMARKS. Cheneval (1984) transferred this species to the genus *Miopelecanus,* which he established for *Pelecanus gracilis* Milne-Edwards 1867 from the Lower Miocene (MN 2) of France. He indicated that the two species might be synonymous.

Pelecanus fraasi Lydekker 1891

Pelecanus fraasi Lydekker, 1891:44, fig. 10a.

HOLOTYPE. Skull; BMNH 47862.

HORIZON AND LOCALITY. Middle Miocene (MN 6) of Lierheim, Nördlinger Ries (82).

REMARKS. This appears to be a valid species of *Pelecanus* Linnaeus 1758 (Cheneval, 1984).

Family Phalacrocoracidae Bonaparte 1853

Phalacrocorax praecarbo Ammon 1918

Phalacrocorax praecarbo Ammon, 1918:28, fig. 3.

HOLOTYPE. Humeral end of left coracoid; MR, uncatalogued.

HORIZON AND LOCALITY. Middle Miocene (MN 7–8) of Dechbetten (90).

REMARKS. Brodkorb (1980) synonymized *Phalacrocorax praecarbo* with *Ardea* (=*Phalacrocorax*) *brunhuberi* Ammon 1918 from the same horizon and locality. See *Ardea brunhuberi* for further discussion.

Carbo risgoviensis Fraas 1908

Carbo risgoviensis O. Fraas in Engel, 1908:567 (*nomen nudum*).

Order Ardeiformes (Wagler 1830)

Family Plataleidae Bonaparte 1838

Rhynchaeites messelensis Wittich 1899

Rhynchaeites messelensis Wittich, 1899:103, pl. 2, figs. 1–17.

HOLOTYPE. Partial skeleton in a slab; location unknown. Peters (1983:4, fig. 2) selected a nearly complete skeleton in a slab, NFS ME 1045, as a neotype of this species because the holotype appears to have been lost.

HORIZON AND LOCALITY. Middle Eocene of Messel (4).

REMARKS. Wittich (1899) thought that *Rhynchaeites messelensis* was intermediate in morphology and taxonomic position between waders and rails, remarking that a similar position is occupied by the modern genus *Rostratula* Vieillot 1816. This was sufficient for Lambrecht (1933) to include *Rhynchaeites* in the Rostratulidae. Peters (1983) showed that the species actually belongs in the Plataleidae, where *Rhynchaeites messelensis* apparently represents a valid species. The status of *Rhynchaeites* within the Plataleidae has not been evaluated.

Plumumida lutetialis Hoch 1980

Plumumida lutetialis Hoch, 1980:40, figs. 2–6.

HOLOTYPE. Incomplete skeleton in a slab; GIH S.G.P.I. 2183.

HORIZON AND LOCALITY. Middle Eocene of Messel (4).

REMARKS. *Plumumida lutetialis* is a synonym of *Rhynchaeites messelensis* Wittich 1899, described from the same horizon and locality (Peters, 1983).

Family Ardeidae Vigors 1825

Ardeacites molassicus Haushalter 1855

Ardeacites molassicus Haushalter, 1855:11, pl. 2, fig. 1.

HOLOTYPE. Right humerus; location unknown.

HORIZON AND LOCALITY. Lower Miocene (MN 3) of Harbatshofen (55).

REMARKS. Brodkorb (1980:91) relegated this species to Aves *incertae sedis,* stating that it is not a heron but that he was "... unable to get it in an order, much less a family."

Botaurites avitus Ammon 1918

Botaurites avitus Ammon, 1918:31, figs. 5, 6.

HOLOTYPE. Cervical vertebra; MR, uncatalogued.

HORIZON AND LOCALITY. Middle Miocene (MN 7–8) of Dechbetten (90).

REMARKS. Olson (1985:67) determined that the holotype of this species is "almost certainly from a cormorant" of the size of *Ardea* (=*Phalacrocorax*) *brunhuberi* Ammon 1918 from the same horizon and locality, and he suggested that *Botaurites avitus* is best synonymized with that species.

Ardea similis Fraas 1870

Ardea similis Fraas, 1870:284, pl. 7, fig. 14a–c.
Botaurites similis: Lambrecht, 1933:315 (new combination).

HOLOTYPE. Distal end of right tibiotarsus; SMNS, uncatalogued.

HORIZON AND LOCALITY. Middle Miocene (MN 7) of Steinheim (87).

REMARKS. Lambrecht (1933:315) thought he saw similarities between the holotype of *Ardea similis* and the same element of the modern ardeid genus *Botaurus* Stephens 1819. He transferred *Ardea similis* to the extinct, supposedly also bittern-like genus *Botaurites* Ammon 1918. Brodkorb (1963:282) followed him, but Olson (1985:166), restudying the figure of the holotype, concluded that "this specimen is from a large phasianid, possibly *Miophasianus altus* [Milne-Edwards (1869)]" described from the Middle Miocene of France.

Ardea brunhuberi Ammon 1918

Ardea brunhuberi Ammon, 1918:30, fig. 4.

HOLOTYPE. Proximal end of left carpometacarpus; MR, uncatalogued.

HORIZON AND LOCALITY. Middle Miocene (MN 7–8) of Dechbetten (90).

REMARKS. Brodkorb (1980) determined that this is actually

a species of cormorant that may be valid, or which may be synonymous with *Graculus* (=*Phalacrocorax*) *intermedius* Milne-Edwards 1867, described from the Middle Miocene (MN 6) of France. I prefer the latter because the slight difference in age between *Phalacrocorax intermedius* and *P. brunhuberi* does not itself substantiate specific separation of the two taxa and the slight difference in size between the two species (Brodkarb, 1980) may easily be attributed to intraspecific variability.

Ardea lignitum Giebel 1860

Ardea lignitum Giebel, 1860:152, pl. 1, fig. 2.
Bubo lignitum: Brodkorb, 1980:90 (new combination).

HOLOTYPE. Distal end of left femur; location unknown.
HORIZON AND LOCALITY. Middle Pliocene (MN 15–16) of Rippersroda 1 (106).
REMARKS. Brodkorb (1980) showed that this is actually an owl of the modern genus *Bubo* Duméril 1806, similar in size and morphology to the modern European Eagle-Owl, *Bubo bubo* (Linnaeus 1758). Because he thought that the specimen came from the Sarmatian (Middle Miocene), he considered *Bubo lignitum* a valid species. Because it is, in fact, much younger, I synonymize it here with the modern *B. bubo.*

Ardea effosa Meyer 1883

Ardea effosa Meyer in Lepsius, 1883:146 (*nomen nudum*).
Ardea effosa Meyer in Lepsius, 1892:623 (*nomen nudum*).

Ardea latipes Meyer 1883

Ardea latipes Meyer in Lepsius, 1883:146 (*nomen nudum*).
Ardea latipes Meyer in Lepsius, 1892:623 (*nomen nudum*).

Family Palaelodidae Stejneger 1885

Palaelodus steinheimensis Fraas 1870

Palaelodus steinheimensis Fraas, 1870:285, pl. 7, fig. 13.

HOLOTYPE. Distal end of left tibiotarsus; SMNS, uncatalogued.
HORIZON AND LOCALITY. Middle Miocene (MN 7) of Steinheim (87).
REMARKS. This is a large anseriform, according to Olson and Feduccia's (1980) reexamination of its description and the figure in Fraas (1870).

Family Phoenicopteridae Bonaparte 1831

Juncitarsus merkeli Peters 1987

Juncitarsus merkeli Peters, 1987b:141, figs. 1, 3–8.

HOLOTYPE. Skeleton on slab; KD, uncatalogued.
HORIZON AND LOCALITY. Middle Eocene of Messel (4).

Order Anseriformes Linnaeus 1758

Family Anseridae Vigors 1825

Cygnavus senckenbergi Lambrecht 1931

Cygnavus senckenbergi Lambrecht, 1931:3, pl. 1, figs. 3, 4; pl. 2, figs. 9–12.

SYNTYPES. Left femur with abraded ends, distal end of left tibiotarsus and pedal phalanx; NFS, uncatalogued.
HORIZON AND LOCALITY. Lower Miocene (MN 2) of Wiesbaden (50).
REMARKS. This species is based on three rather undiagnostic elements, and it was probably their size alone that led Lambrecht (1931, 1933) and others (Brodkorb, 1964; Howard, 1964) to consider it a swan. However, the syntype femur differs from the same element of Anserinae in having the border of condylus lateralis less extended cranially. Although the species appears to be correctly assigned to the Anseriformes, there is little information as to its taxonomic position within that order, and until restudied it should be relegated to Anseriformes *incertae sedis.*

Cygnus csakvarensis Lambrecht 1933

Cygnus csákvárensis Lambrecht, 1931:4 (*nomen nudum*).
Cygnus csákvárensis Lambrecht, 1933:283, fig. 128g, h.
Cygnanser csákvárensis: Kretzoi, 1957:240 (new combination).
Cygnanser csakvarensis: Brodkorb, 1964:210 (spelling emended).
Olor csakvarensis Mlíkovský, this paper (new combination).

LECTOTYPE. Proximal end of left carpometacarpus; GIB, uncatalogued; selected by Kretzoi (1957:240).
PARALECTOTYPES. Distal end of right carpometacarpus, phalanx 1 digiti majoris; GIB, uncatalogued. All syntypes are figured in Kretzoi (1957:figs. 37–43).
HORIZON AND LOCALITY. Upper Miocene (MN 10) of Csákvár (96).
REMARKS. Based on a study of two referred elements, an anterior portion of a sternum and fragmentary dentale, from the same horizon and locality, Kretzoi (1957) concluded that *Cygnus csakvarensis* was intermediate in morphology between *Cygnus* Bechstein 1802 and *Anser* Brisson 1760 and created a new genus, *Cygnanser,* for it. This action seems unsubstantiated because the lectotype carpometacarpus agrees well with the same element of swans. Moreover, it differs from the same element of *Cygnus* (*sensu stricto*) and agrees with that of *Olor* Wagler 1832 in having the following: (1) fovea carpalis caudalis shallow, and (2) facies dorsalis ossis metacarpalis allularis less deepened. With no evidence to the contrary, I consider *Olor csakvarensis* (Lambrecht) new combination a valid species.

Cygnus bilinicus Laube 1909

Cygnus bilinicus Laube, 1909:161, pl. I.

HOLOTYPE. Proximal end of ulna, proximal end of radius and carpometacarpus, lacking processus extensorius, in a slab; all apparently from a single individual. The bones are too flattened to reveal from which side of the body they originated. RMT, uncatalogued.

HORIZON AND LOCALITY. Lower Miocene (?MN 3) of Břešťany (59).

REMARKS. Lambrecht (1933) and others (Howard, 1964; Brodkorb, 1978) thought that *Cygnus bilinicus* is actually a raptor, but a restudy of the holotype showed that it is an indeterminate stork, family Ciconiidae (Mlíkovský and Švec, 1989).

Anas cygniformis Fraas 1870

Anas cygniformis Fraas, 1870:276, pl. 13, fig. 2a, b.
Anser cygniformis: Lambrecht, 1933:369 (new combination).

LECTOTYPE. Left coracoid, figured in Fraas (1870:pl. 13, fig. 2a, b); selected here. SMNS, uncatalogued.

PARALECTOTYPES. Two tarsometarsi and 3 pedal phalanges; SMNS, uncatalaogued.

HORIZON AND LOCALITY. Middle Miocene (MN 7) of Steinheim (87).

REMARKS. Lambrecht (1933) transferred *Anas cygniformis* to the modern genus *Anser* Brisson 1760 on the basis of more developed lineae intermusculares on the impressio musculi sternocoracoidei. This character is not valid according to my observations, but other aspects of the lectotype coracoid support Lambrecht's (1933) judgment. The angle between the axis of the corpus coracoidei and the sternal facet, a blunt angulus medialis, and the presence of foramina pneumatica under the facies articularis clavicularis coracoidei are sufficient to refer *Anas cygniformis* to the Anserinae. Within that subfamily, the lectotype coracoid differs from the same element of the Cygnini and agrees with that of the Anserini in having the following: (1) canalis triosseus between the processus procoracoideus and the lateral border of the processus acrocoracoideus deep, and (2) foramina pneumatica under the facies articularis clavicularis coracoidei larger and limited to the lateral side of the sulcus musculi supracoracoidei. The latter character, and the fact that facies articularis clavicularis coracoidei appears less clearly bordered by the canalis triosseus, is sufficient to allocate *Anas cygniformis* to the genus *Anser*.

The specific status of *Anser cygniformis* is much less certain because *Anas* (=*Anser*) *oeningensis* Meyer 1865 (see below), described from a similarly aged (MN 7), nearby deposit is about the same size. Direct comparison is presently impossible, so I hesitate to synonymize the former with the latter, but the possibility that *Anser cygniformes* is not a valid species should be kept in mind in future studies.

Anas oeningensis Meyer 1865

Anas oeningensis Meyer, 1865:126, pl. 30, fig. 2.
Anser oeningensis: Milne-Edwards, 1867:127 (new combination).

HOLOTYPE. Incomplete skeleton in a slab, including a sternum, partial scapulae, sternal end of coracoid, humeri, ulnae, radii, distal end of carpometacarpus, phalanx 1 digiti majoris, and rib fragments; BMNH 42804.

HORIZON AND LOCALITY. Middle Miocene (MN 7) of Öhningen (86).

REMARKS. Milne-Edwards (1867:127–28) transferred this species to the modern genus *Anser*. The shape of the spina externa sterni and the position of the dorsal linea intermuscularis sterni, which are quite visible in Meyer's (1865) illustration of the holotype, clearly support this decision. *Anser oeningensis* appears to be a valid species of goose.

Anas basaltica Bayer 1882

Anas (?)*basaltica* Bayer, 1882:20, fig. 8/1.
Anas (?)*basaltica* Bayer, 1883:62, fig. 1 (here labeled "n. sp.").

HOLOTYPE. Imprints of right coracoid lacking facies articularis sternalis, proximal end of right humerus, cranial end of right scapula, and a rib fragment, probably all from a single individual; NMP ČM 1519. See Mlíkovský and Švec (1989) for additional information.

HORIZON AND LOCALITY. Middle Oligocene of Varnsdorf (22).

REMARKS. This is an indeterminate heron of the tribe Ardeini (Mlíkovský and Švec, 1989).

Anas skalicensis Bayer 1882

Anas (?)*skalicensis* Bayer, 1882:21, fig. 8/2.
Anas (?)*skalicensis* Bayer, 1883:64, fig. 2 (here labeled "n. sp.").

HOLOTYPE. Scraps of long bones; NMP ČM 1520.

HORIZON AND LOCALITY. Middle Oligocene of Skalice (23).

REMARKS. The holotype of this species is indeterminate, even at the ordinal level (Mlíkovský and Švec, 1989).

Anas isarensis Lambrecht 1933

Anas isarensis Lambrecht, 1933:361, fig. 123a.

HOLOTYPE. Cranial end of right scapula; BSP 1926 v 12b.

HORIZON AND LOCALITY. Middle/Upper Miocene (MN 8–9) of Aumeister (91).

REMARKS. As seen in the original illustration, the holotype scapula differs from the same element of Anatini and agrees with that of Aythyini in having the following: (1) acromion more slender, (2) acromion more perpendicular to the axis of scapula, (3) whole extremitas cranialis more slender, and (4) longitudinal furrow on the facies costalis between tuberculum coracoideum and acromion deeper. Within Aythyini, however, the scapula is indeterminate (Woolfenden, 1961), so *Anas isarensis* will remain as Aythyini *incertae sedis*.

Anas risgoviensis Ammon 1918

Anas risgoviensis Ammon, 1918:41, unfigured.

SYNTYPES. Left and right coracoids; BMNH 48165 and 48165a.

HORIZON AND LOCALITY. Middle Miocene (MN 6) of Lierheim, Nördlinger Ries (82).

REMARKS. This is nearly a *nomen nudum*. Until the syntypes of *Anas risgoviensis* are restudied, it should be considered Aves *incertae sedis* (see also Cheneval, 1987:147).

Anas eppelsheimensis Lambrecht 1933

Anas eppelsheimensis Lambrecht, 1933:362, fig. 124.

HOLOTYPE. Right coracoid, lacking extremitas sternalis and processus acrocoracoideus; ZGIB, uncatalogued.

HORIZON AND LOCALITY. Upper Miocene (MN 9) of Eppelsheim (94).

REMARKS. Based on a study of the figure of the holotype in Lambrecht (1933), I consider this fossil indeterminate at even the tribal level within the Anseridae and thus relegate *Anas eppelsheimensis* to Anseridae *incertae sedis*.

Anas meyerii Milne-Edwards 1867

Anas meyerii Milne-Edwards, 1867:129, unfigured.
Aythya meyerii: Brodkorb, 1964:228 (new combination).

HOLOTYPE. Crushed tarsometatarsus with associated phalanges in a slab; BMNH 42805.

HORIZON AND LOCALITY. Middle Miocene (MN 7) of Öhningen (86).

REMARKS. Both Meyer (1865), who described and figured the specimen, and Milne-Edwards (1867), who named the species, mentioned the badly crushed state of the holotype. It is quite possible that the figure in Meyer (1865) is a reconstruction. Brodkorb (1964) transferred the species to the modern genus *Aythya* Boie 1822, probably inspired by Milne-Edwards' (1867) remark that the specimen exhibits some similarities to the same element of Fuligules (=Aythyini). This is a doubtful action and I recommend considering *Anas meyerii* as Aves *incertae sedis* until the holotype is restudied. There is a high probability that the species will be found to be based upon indeterminate remains.

Anas albae Jánossy 1979

Anas albae Jánossy, 1979:16, unfigured.

HOLOTYPE. Left carpometacarpus, NMB Vt.84.

HORIZON AND LOCALITY. Upper Miocene (MN 13) of Polgárdi (100).

REMARKS. The holotype of *Anas albae* was originally determined by V. Čapek (in Lambrecht, 1912a, 1912b) as "*Mergus* sp." Jánossy (1979) placed the species in the modern genus *Anas* Linnaeus 1758.

Anas atava Fraas 1870

Anas atava Fraas, 1870:275, pl. 13, fig. 1a–c.
Anser atavus: Lambrecht, 1933:369 (new combination).
Cygnus atavus: Mlíkovský, this paper (new combination).

HOLOTYPE. Proximal end of right femur; SMNS, uncatalogued.

HORIZON AND LOCALITY. Middle Miocene (MN 7) of Steinheim (87).

REMARKS. Lambrecht (1933) transferred *Anas atava* to the modern genus *Anser,* but, as judged from the illustrations in Fraas (1870), the holotype femur differs from the same element of Anserini and agrees with that of Cygnini in having the following: (1) processus trochantericus inclined in norma caudalis, and (2) collum femoris more reduced. The latter character, and the transverse ridge on the facies articularis antitrochanterica, is sufficient to distinguish the specimen from the same element of *Olor* and to refer it to *Cygnus* (*sensu stricto*). Here, *Cygnus atavus* (Fraas) new combination is probably a valid species.

Anas submajor Jánossy 1979

Anas submajor Jánossy, 1979:11, fig. 4/2.

HOLOTYPE. Left ulna; NMB Vt.83.

HORIZON AND LOCALITY. Upper Pliocene (MN 17) of Villány Mountains. Exact locality was not given by Jánossy (1979), but it was probably Villány 3 (115).

REMARKS. This species belongs to the modern genus *Tadorna* Oken 1817, where it is inseparable from, and synonymous with, the extant *Tadorna tadorna* (Linnaeus 1758) (Mlíkovský, 1982).

Order Falconiformes Sharpe 1874

Family Vulturidae Illiger 1811

Eocathartes robustus Lambrecht 1935

Eocathartes robustus Lambrecht, 1935:362, pl. 18, fig. 2.

HOLOTYPE. Partial skeleton in a slab, including pelvis, left and right femur, right tibiotarsus, right tarsometatarsus, and associated basal phalanges of toes II–IV; GM 6883.

HORIZON AND LOCALITY. Middle Eocene of Geisel Valley (5).

REMARKS. According to Houde (in Olson, 1985:191), this is almost certainly not a vulturid, but its true affinities are still unclear.

Order Galliformes Linnaeus 1758

Family Gallinuloididae Lucas 1900

Taoperdix miocaena Ballmann 1969

Taoperdix miocaena Ballmann, 1969:29, pl. II, fig. 14a, b.

HOLOTYPE. Proximal end of left carpometacarpus; BSP 18111.

HORIZON AND LOCALITY. Lower Miocene (MN 3) of Wintershof (West) (56).

Family Tetraonidae Vigors 1825

Tetrao macropus Jánossy 1976

Tetrao macropus Jánossy, 1976a:17, pl. I, fig. 6.

HOLOTYPE. Distal end of left tibiotarsus; GIB V.10348.

HORIZON AND LOCALITY. Lower Pliocene (MN 15) of Csarnóta 2 (105).

Tetrao conjugens Jánossy 1974

Tetrao conjugens Jánossy, 1974b:537, pl. 23, fig. 9.

HOLOTYPE. Proximal end of left carpometacarpus; IZK, uncatalogued.

HORIZON AND LOCALITY. Lower Pliocene (MN 15) of Węże 1 (101).

Lagopus lagopus atavus Jánossy 1974

Lagopus lagopus atavus Jánossy, 1974b:534, pl. 24, figs. 4–8.
Lagopus atavus: Jánossy, 1976a:33 (new rank).

SYNTYPES. Thirty-three bone fragments, listed in Jánossy (1974b:534); IZK, uncatalogued.

HORIZON AND LOCALITY. Upper Pliocene (MN 16) of Rębielice Królewskie 1 (107).

REMARKS. Jánossy (1976a) elevated this subspecies to the species rank, but since the Willow Grouse, *Lagopus lagopus* (Linnaeus 1758), was rather variable in the late Cenozoic (Bocheński, 1974, 1985; Potapova, 1986), its taxonomic validity should be reevaluated.

Family Phasianidae Vigors 1825

Palaeortyx intermedia Ballmann 1969

Palaeortyx (?)*intermedia* Ballmann, 1969:33, pl. 1, figs. 1, 2.

HOLOTYPE. Left coracoid; BSP 18103.
HORIZON AND LOCALITY. Lower Miocene (MN 3) of Wintershof (West) (56).

Phasianus augustus Ammon 1918

Phasianus augustus Ammon, 1918:45, figs. 9, 10.
Miophasianus augustus: Lambrecht, 1933:440 (new combination).

HOLOTYPE. Left femur; MR, uncatalogued.
HORIZON AND LOCALITY. Middle Miocene (MN 7–8) of Dechbetten (90).
REMARKS. This species was transferred to *Miophasianus* by Lambrecht (1933). It was subsequently synonymized with *Phasianus* (=*Miophasianus*) *altus* Milne-Edwards 1871, described from the Middle Miocene (MN 6) of France (Švec, 1986; Bocheński, 1987).

Gallus longaevus Ammon 1918

Gallus longaevus Ammon, 1918:41, fig. 8.
Miogallus longaevus: Lambrecht, 1933:442 (new combination).

HOLOTYPE. Humeral end of left coracoid; MR, uncatalogued.
HORIZON AND LOCALITY. Middle Miocene (MN 7–8) of Dechbetten (90).
REMARKS. Ammon (1918) was unable to determine the affinities of this species within the Phasianidae and decided to place it ". . . in the best known genus *Gallus*, which in the present case is to be understood in its broadest sense, so to say as a group name" [my translation]. Lambrecht (1933), without seeing the holotype, established the genus *Miogallus* for *G. longaevus* because of its great age. *Gallus longaevus* is obviously Aves *incertae sedis* until its holotype is restudied.

Gallus beremendensis Jánossy 1976

Gallus beremendensis Jánossy, 1976b:34, fig. 8/5.

HOLOTYPE. Right humerus; GIB, uncatalogued.
HORIZON AND LOCALITY. Upper Pliocene (MN 17) of Beremend 5 (116).

Gallus steinheimensis Fraas 1908

Gallus steinheimensis E. Fraas in Engel, 1908:567 (*nomen nudum*).

REMARKS. Brodkorb (1978:222) attributed this species to Theodor Fraas (probably *lapsus calami*), but Engel (1908) wrote E. Fraas, which apparently means Eberhard Fraas, son of Oskar Fraas.

Alectoris bavarica Ballmann 1969

Alectoris bavarica Ballmann, 1969:36, pl. 1, fig. 4a, b.

HOLOTYPE. Left tarsometatarus; BSP 18110.
HORIZON AND LOCALITY. Lower Miocene (MN 3) of Wintershof (West) (56).

Francolinus subfrancolinus Jánossy 1976b

Francolinus subfrancolinus Jánossy, 1976b:36, fig. 8/3.

HOLOTYPE. Left carpometacarpus, lacking os metacarpale minus; GIB, uncatalogued.
HORIZON AND LOCALITY. Upper Pliocene (MN 17) of Villány 3 (115).

Francolinus capeki wenzensis Jánossy 1974

Francolinus capeki wenzensis Jánossy, 1974b:540, pl. 23, figs. 7, 8.
Francolinus wezensis [*sic*]: Jánossy, 1981:380 (new rank).

SYNTYPES. Thirty-four bones and bone fragments, listed in Jánossy (1974b:540).
HORIZON AND LOCALITY. Lower Pliocene (MN 15) of Węże 1 (101).

REMARKS. *Francolinus capeki wenzensis* was described as a temporal and geographical subspecies of *F. capeki* Lambrecht 1933, from the lower Pleistocene (Biharian) of northwest Rumania. The taxonomic position of these birds should be reevaluated because they differ markedly from modern francolins in lacking a spur on the tarsometatarsus.

Francolinus capeki villanyiensis Jánossy 1974

Francolinus capeki villányiensis Jánossy, 1974b:540, pl. 23, figs. 1–6.
Francolinus capeki villanyiensis: Mlíkovský, this paper (spelling emended).

SYNTYPES. 226 bones and bone fragments, listed in Jánossy (1974b:540).
HORIZON AND LOCALITY. Upper Pliocene (MN 16) of Rębielice Królewskie 1 (107).

REMARKS. The subspecific name was spelled with a long-sign above the *a* in the original description. As this is not allowed by Article 32 of the International Code of Zoological Nomenclature (ICZN, 1985), I here emend the spelling to *villanyiensis*.
Francolinus capeki villanyiensis was described as a temporal subspecies of *Francolinus capeki* Lambrecht 1933, younger than *Francolinus capeki wenzensis* Jánossy (1974b).

Francolinus minor Jánossy 1974

Francolinus (*Lambrechtia*) *minor* Jánossy, 1974b:547, unfigured.

HOLOTYPE. Left carpometacarpus, lacking os metacarpale minus; IZK, uncatalogued.
HORIZON AND LOCALITY. Upper Pliocene (MN 16) of Rębielice Królewskie 2 (108).

Order Gruiformes Bonaparte 1854

Family Messelornithidae Hesse 1988

Messelornis cristata Hesse 1988

Messelornis cristata Hesse, 1988:90, figs. 15–17.

HOLOTYPE. Complete skeleton in three plates; NFS ME 807a–c.

HORIZON AND LOCALITY. Middle Eocene of Messel (4).

Family Gruidae Vigors 1825

Pliogrus germanicus Lambrecht 1933

Pliogrus germanicus Lambrecht, 1933:522, fig. 156.
Palaelodus germanicus: Fischer and Stephan, 1971:576 (new combination).

HOLOTYPE. Distal end of left tibiotarsus; ZGIB, uncatalogued.

HORIZON AND LOCALITY. Upper Miocene (MN 9) of Eppelsheim (94).

REMARKS. Fischer and Stephan (1971) transferred this species to the flamingo genus *Palaelodus* Milne-Edwards 1863 and hypothesized that it might even be synonymous with *Palaelodus ambiguus* Milne-Edwards 1871 from the Lower Miocene (MN 2) of France. The species is in need of reexamination.

Family Rallidae Vigors 1825

Pararallus hassenkampi Martini 1967

Pararallus hassenkampi Martini, 1967a:8, unfigured (*nomen nudum*).
Pararallus hassenkampi Martini, 1967b:289, text-fig. 1, pl. 29, figs. 1, 2.

HOLOTYPE. Distal end of left tarsometatarsus with associated proximal phalanges digitorum I–IV (in a slab and counterslab); GPIW F 1237 and F 1238.

HORIZON AND LOCALITY. Lower Oligocene of Sieblos (13).

REMARKS. This is apparently not a rail (Cracraft, 1973; Olson, 1977), but its affinities have not yet been clarified.

Microrallus fejfari Švec 1983

Microrallus fejfari Švec, 1983:37, fig. 1a.

HOLOTYPE. Distal end of left humerus; DP FNSP 4818.

HORIZON AND LOCALITY. Lower Miocene (MN 4) of Dolnice 2 (67).

Porzana estramosi Jánossy 1979

Porzana estramosi Jánossy, 1979:20, fig. 4/8.

HOLOTYPE. Fragmentary distal end of left tarsometatarsus; GIB V.78120.

HORIZON AND LOCALITY. Lower Pliocene (MN 15) of Osztramos 9 (104).

REMARKS. Jánossy (1979) placed this species in the modern rallid genus *Porzana* Vieillot 1816 solely on the basis of its small size. This is clearly insufficient. The diagnosis and the description of the species do not include any usable morphological details, and because the figure is indistinct, *Porzana estramosi* should be treated as Aves *incertae sedis* until the holotype is restudied.

Table 1. Leg proportions [tibiotarsus length : tarsometatarsus length (tt:tmt)] in *Otis affinis* and modern genera of bustards.

	Number of species (individuals)	tt:tmt
Otis affinis	1 (1)	1.42[a]
Otis	2 (4)	1.36–1.50
Chlamydotis	1 (2)	1.29–1.36
Eupodotis	6 (9)	1.21–1.38
Ardeotis	1 (1)	1.25
Neotis	2 (2)	1.22–1.25

[a] My estimation based on the figure of the holotype in Lambrecht (1933: 529). Other values were recalculated from Verheyen (1957) and Jánossy (1972).

Family Phorusrhacidae Ameghino 1899

Aenigmavis sapea Peters 1987

Aenigmavis sapea Peters, 1987a:73, figs. 1–12.

HOLOTYPE. Partial skeleton in a slab; UM, uncatalogued.

HORIZON AND LOCALITY. Middle Eocene of Messel (4).

Family Otididae Gray 1840

Otis affinis Lydekker 1891

Otis affinis Lydekker, 1891:168, unfigured.
Chlamydotis affinis: Brodkorb, 1967:174 (new combination).

HOLOTYPE. Crushed postcranial skeleton in a slab; BMNH 36745. See Lambrecht (1933:fig. 157b) for its illustration.

HORIZON AND LOCALITY. Middle Miocene (MN 7) of Steinheim (87), according to Ammon (1918) who considered Lydekker's (1891) note that the holotype originated from the Lower Miocene (MN 3) of nearby Schnaitheim incorrect.

REMARKS. Brodkorb (1967) placed this species in the modern genus *Chlamydotis* Lesson 1839, possibly on the basis of Lydekker's (1891) erroneous remarks that the fossil has the exact proportions of *Otis* (=*Chlamydotis*) *undulata* (Jacquin 1784). Actually, the leg proportions of *Otis affinis* differ markedly from those of *Chlamydotis undulata* and agree best with those of *Otis* Linnaeus 1758 (Table 1). Thus, until the holotype is restudied, the species is best treated as a member of the latter genus.

Order Diatrymiformes Matthew and Granger 1917

Family Diatrymidae Matthew and Granger 1917

Diatryma geiselensis Fischer 1978

Diatryma geiselensis Fischer, 1978:134, unfigured.

HOLOTYPE. Right scapulocoracoid; GM ?/Dia.2. See Fischer (1962:fig. 2) for an illustration of the holotype.

HORIZON AND LOCALITY. Middle Eocene of Geisel Valley (5).

REMARKS. This species deserves, as do all diatrymas, a modern revision (cf. Olson, 1985).

Order Charadriiformes Huxley 1867

Family Scolopacidae Vigors 1825

Totanus praecursor Laube 1901

Totanus praecursor Laube, 1901:66, fig. 14.

HOLOTYPE. Pelvic impression; location unknown. The holotype is not in the Dresden Museum, where it should perhaps have been deposited (Lambrecht, 1933:538), but never was (S. Eck, in litt., 1987). Neither is it in the National Museum in Praha (J. Beneš, pers. comm., 1985), nor in the Regional Museum in Teplice (D. Ernygrová, pers. comm., 1986) where other bird remains from the same locality are deposited.

HORIZON AND LOCALITY. Lower Miocene (?MN 3) of Břešťany (59).

REMARKS. As the holotype appears to have been lost, and its figure in Laube (1901) is less than informative, I relegate *Totanus praecursor* to Aves *incertae sedis* until such time as the holotype is found and restudied.

Scolopax baranensis Jánossy 1979

Scolopax baranensis Jánossy, 1979:23, unfigured.

HOLOTYPE. Proximal end of carpometacarpus (body side not given); NMB Vt.82.

HORIZON AND LOCALITY. Lower Pliocene (MN 15) of Csarnóta 2 (105).

REMARKS. Jánossy's (1979) superficial and irrelevant description of this species makes it almost a *nomen nudum*. In any case, *Scolopax baranensis* belongs in Aves *incertae sedis* until its holotype is restudied.

Gallinago veterior Jánossy 1979

Gallinago veterior Jánossy, 1979:24, fig. 4/9.

HOLOTYPE. Nearly complete right coracoid; NMB Vt.81. Jánossy (1979) stated that the holotype is from the left side of the body, but the figure shows a right coracoid.

HORIZON AND LOCALITY. Lower Pliocene (MN 15) of Csarnóta 2 (105).

REMARKS. *Gallinago veterior* is almost a *nomen nudum* because of the entirely useless diagnosis and nearly useless description given by Jánossy (1979). Until the holotype is restudied, the species is best referred to Aves *incertae sedis*.

Family Glareolidae Brehm 1831

Mioglareola gregaria Ballmann 1979

Mioglareola gregaria Ballmann, 1979:68, text-fig. 3, pl. 1, figs. 3–5.

HOLOTYPE. Skull; BSP 1970 XVIII 851.

HORIZON AND LOCALITY. Middle Miocene (MN 6) of Steinberg, Nördlinger Ries (82).

Glareola neogaena Ballmann 1979

Glareola neogaena Ballmann, 1979:81, pl. 1, fig. 9; pl. 2, fig. 1.

HOLOTYPE. Right humerus; BSP 1970 XVIII 852.

HORIZON AND LOCALITY. Middle Miocene (MN 6) of Steinberg, Nördlinger Ries (82).

Family Laridae Vigors 1825

Gaviota lipsiensis Fischer 1983

Gaviota lipsiensis Fischer, 1983a:152, pl. XII, figs. 1, 2.

HOLOTYPE. Distal end of right humerus; MB Av.732.

HORIZON AND LOCALITY. Middle Oligocene of Espenhain (21).

Larus dolnicensis Švec 1980

Larus dolnicensis Švec, 1980:380, pl. 1, figs. 2, 3.

HOLOTYPE. Distal end of left humerus; DP FNSP 7344.

HORIZON AND LOCALITY. Lower Miocene (MN 4) of Dolnice 2 (67).

REMARKS. As already recognized by Olson (1985:182), this is not a gull, but a member of the family Glareolidae (Mlíkovský, pers. obs.). I have yet to ascertain its affinities within that family.

Family Alcidae Vigors 1825

Petralca austriaca Mlíkovský 1987

Petralca austriaca Mlíkovský, 1987:136, text-figs. 4, 5, pls. 1, 2.

HOLOTYPE. Incomplete skeleton in a slab and counter-slab, including coracoids and all of the main wing bones; NMW 1980/25.

HORIZON AND LOCALITY. Upper Oligocene of Traun-Pucking (32).

Order Cuculiformes Wagler 1830

Family Cuculidae Vigors 1825

Cuculus csarnotanus Jánossy 1979

Cuculus csarnotanus Jánossy, 1979:25, fig. 4/6.

HOLOTYPE. Distal end of left humerus; NMB Vt.80.

HORIZON AND LOCALITY. Lower Pliocene (MN 15) of Csarnóta 2 (105).

Order Strigiformes Wagler 1830

Family Protostrigidae Wetmore 1933

Oligostrix rupelensis Fischer 1982

Oligostrix rupeliensis Fischer, 1982:152, unfigured (*nomen nudum*).
Oligostrix rupelensis Fischer, 1983b:483, figs. 1, 3, 5, 7, 9.

HOLOTYPE. Distal end of left tibiotarsus; MB Av. 730.
HORIZON AND LOCALITY. Middle Oligocene of Espenhain (21).

Family Strigidae Vigors 1825

Eoglaucidium pallas Fisher 1987

Eoglaucidium pallas Fischer, 1987:138, figs. 1, 4.

HOLOTYPE. Right humerus; GM XXII/761.
HORIZON AND LOCALITY. Middle Eocene of Geisel Valley (5).
REMARKS. I am in the process of studying several more specimens (humeri, coracoids, scapulae) from the same horizon and locality that can clearly be referred to this species. This work is not complete, but it appears that the species may belong to the Coraciiformes and not the Strigiformes.

Bubo florianae Kretzoi 1957

Bubo (?)*florianae* Kretzoi, 1957:243, figs. 47–49.

HOLOTYPE. Phalanx 1 of pedal digit II; GIB, uncatalogued.
HORIZON AND LOCALITY. Upper Miocene (MN 10) of Csákvár (96).

Surnia robusta Jánossy 1977

Surnia robusta Jánossy, 1977:10, fig. 2a–d, 5/10.

HOLOTYPE. Left tarsometatarsus; NMB Vt.62.
HORIZON AND LOCALITY. Upper Pliocene (MN 17) of Villány 3 (115).

Otus wintershofensis Ballmann 1969

Otus wintershofensis Ballmann, 1969:39, pl. 1, fig. 11a, b.

HOLOTYPE. Distal end of right tibiotarsus; BSP 18121.
HORIZON AND LOCALITY. Lower Miocene (MN 3) of Wintershof (West) (56).

Athene noctua veta Jánossy 1974

Athene noctua veta Jánossy, 1974b:555, pl. 24, fig. 1.
Athene veta: Jánossy, 1979:19 (new rank).

HOLOTYPE. Humeral end of right [not left, as stated by Jánossy (1974b)] coracoid; IZK, uncatalogued. The specimen was not designated as holotype of *Athene noctua veta* by Jánossy (1974b); he generally does not select types for his new subspecies. I call it the holotype here because it is the only specimen upon which the taxon was based.
HORIZON AND LOCALITY. Upper Pliocene (MN 16) of Rębielice Królewskie 1 (107).

REMARKS. I have reexamined the holotype and find that it does not belong to the genus *Athene* Boie 1822, but to another modern strigiform genus, *Aegolius* Kaup 1829. The holotype coracoid differs from that of *Athene* and agrees with that of *Aegolius* in having the following: (1) head deflected more mediad in ventral view, (2) head more robust in humeral view, (3) the border between impressio ligamenti acrocoracohumeralis and facies articularis humeralis indistinct (in *Athene* it is distinctly narrowed), and (4) foramen nervi supracoracoidei smaller. The latter character is the primary one in Jánossy's diagnosis of *Athene noctua veta.* Because there are no meaningful morphological or mensural character differences between the holotype coracoid fragment of *Athene noctua veta* (it is not measurable) and the same element of the extant *Aegolius funereus* (Linnaeus 1758), the only representative of the genus in the Palearctic, I here synonymize the *Athene noctua veta* Jánossy (1974) with the latter species.

Strix brevis Ballmann 1969

Strix brevis Ballmann, 1969:38, pl. 1, fig. 7a, b.

HOLOTYPE. Distal end of left humerus; BSP 18012.
HORIZON AND LOCALITY. Lower Miocene (MN 3) of Wintershof (West) (56).

Order Apodiformes Peters 1940

Family Aegialornithidae Lydekker 1891

Aegialornis szarskii Peters 1985

Aegialornis szarskii Peters, 1985:144, figs. 1, 4a, b.
Primapus szarskii: Mourer-Chauviré, 1988:372 (new combination).

HOLOTYPE. Nearly complete skeleton in a slab; NFS LNK-Me 301.
HORIZON AND LOCALITY. Middle Eocene of Messel (4).

Family Apodidae Hartert 1897

Chaetura baconica Jánossy 1977

Chaetura baconica Jánossy, 1977:22, fig. 5/13.

HOLOTYPE. Right ulna; NMB Vt.64.
HORIZON AND LOCALITY. Upper Miocene (MN 11–12) of Sümeg (98).

Order Coraciiformes Forbes 1884

Family Bucerotidae Vigors 1825

Geiseloceros robustus Lambrecht 1935

Geiseloceros robustus Lambrecht, 1935:365, pl. 2.

HOLOTYPE. Partial skeleton in a slab, including more or less complete left and right coracoids, right scapula, left and right humeri, right ulna, right radius, right carpometacarpus, phalanx 1 of right digitus major, and phalanx of right digitus minor; GM 5884.
HORIZON AND LOCALITY. Middle Eocene of Geisel Valley (5).
REMARKS. The wing proportions of *Geiseloceros robustus* (ulna shorter than humerus) make it highly improbable that this species is a hornbill (Olson, 1985), all of which possess ulnae

markedly longer than humeri (Verheyen, 1955). The true systematic position of this species remains uncertain, although Houde (in Olson, 1985) suggested that it may possibly be identical with *Eocathartes robustus* Lambrecht 1935, an alleged vulture described from the same horizon and locality.

Order Piciformes Meyer and Wolf 1810

Family *incertae sedis*

Zygodactylus ignotus Ballmann 1969

Zygodactylus ignotus Ballmann, 1969:52, pl. 2, fig. 13a, b.

HOLOTYPE. Distal end of right tarsometatarsus; BSP 18164.
HORIZON AND LOCALITY. Lower Miocene (MN 3) of Wintershof (West) (56).
REMARKS. Brodkorb (1971:257) created a new family, Zygodactylidae, for this species. Its affinities, however, still appear to be unclear (Olson, 1985:121–22).

Family Capitonidae Bonaparte 1840

Capitonides europeus Ballmann 1969

Capitonides europeus Ballmann, 1969:44, pl. 2, fig. 1a, b.

HOLOTYPE. Right carpometacarpus; BSP 18162.
HORIZON AND LOCALITY. Lower Miocene (MN 3) of Wintershof (West) (56).
REMARKS. In spite of a thorough original description, the genus *Capitonides* Ballmann 1969, which is based on *C. europeus*, was never properly diagnosed. To the contrary, Ballmann (1983) stressed its similarities to the modern genus *Trachyphonus* Vieillot 1816. The possibility that *Capitonides* is synonymous with *Trachyphonus* should be evaluated (but see Prum, 1988).

Capitonides protractus Ballmann 1983

Capitonides protractus Ballmann, 1983:46, figs. 2/5-6, 3a–d.

HOLOTYPE. Right tarsometatarsus; BSP 1970 XVIII.
HORIZON AND LOCALITY. Middle Miocene (MN 6) of Steinberg, Nördlinger Ries (82).
REMARKS. See *Capitonides europeus* for the generic status of this species.

Family Picidae Vigors 1825

Dendrocopos praemedius Jánossy 1974

Dendrocopos praemedius Jánossy, 1974a:237, unfigured.

HOLOTYPE. Right carpometacarpus; GIB, uncatalogued.
HORIZON AND LOCALITY. Upper Pliocene (MN 17) of Villány 3 (115).

Order Passeriformes Linnaeus 1758

Family *incertae sedis*

Protornis glarniensis Meyer 1844

Osteornis scolopacinus Gervais, 1844:39, unfigured (*nomen nudum*).
Protornis glarniensis Meyer, 1844:338, unfigured.
Protornis glarisiensis Anonymous, 1844:v, unfigured (*nomen nudum*).
Protornis glaronensis Meyer, 1856:92, pl. XV, fig. 12 (unjustified emendation of *Protornis glarniensis* and consequently its objective synonym).

HOLOTYPE. Incomplete skeleton in a slab and counter-slab; MZ, uncatalogued.
HORIZON AND LOCALITY. Lower Oligocene of Matt (12).
REMARKS. This species was originally described as a passerine bird (*sensu lato*) by Meyer (1839b, 1844, 1856). It was later transferred to the Alcedinidae (Peyer, 1957; Storer, 1960; Brodkorb, 1971) but has more recently been placed with the Momotidae (Olson, 1976).

Protornis blumeri Heer 1865

Protornis blumeri Heer, 1865:236, fig. 143 (reprinted in Peyer, 1957:fig. 25).

HOLOTYPE. Partial skeleton impression in a slab; location unknown.
HORIZON AND LOCALITY. Lower Oligocene of Matt (12).
REMARKS. After studying the figure and description of this fossil by Heer (1865), I can only agree with Olson (1976:117) that *Protornis blumeri* ". . . should be relegated to the category of Aves incertae sedis . . ." until its holotype is located and restudied.

Family Timaliidae Gray 1841

Turdoides borealis Jánossy 1979

Turdoides borealis Jánossy, 1979:27, fig. 4/7.

HOLOTYPE. Proximal part of left humerus; GIB V.78119.
HORIZON AND LOCALITY. Lower Pliocene (MN 15) of Osztramos 1 (103).
REMARKS. This species is based upon a badly eroded, fragmentary humerus that is unsuitable for identification. Moreover, even if Jánossy (1979) correctly assigned the fossil to the turdoidine timalias, its generic affiliation is doubtful because he compared it with only 3 of the 38 extant genera of this subfamily (*sensu* Wolters, 1975–1982). I consider *Turdoides borealis* as Aves *incertae sedis* until its holotype is restudied.

Aves *incertae sedis*

Eleutherornis helveticus Schaub 1940

Eleutherornis helveticus Schaub, 1940a:283, figs. 1–4.

HOLOTYPE. Anterior portion of a pelvis; NHMB Eh 781.
HORIZON AND LOCALITY. Middle Eocene of Egerkingen (6).
REMARKS. Schaub (1940a) conjectured that this may have been a ratite bird (*sensu lato*). Wetmore (1951) created a separate family, the Eleutherornithidae, for it, which he considered closely related to the Struthionidae (see also Brodkorb, 1963; Cracraft, 1974). Although this arrangement may prove to be correct, it seems advisable to consider *Eleutherornis helveticus* as *incertae sedis* until its holotype is restudied and compared with other giant Paleocene and Eocene birds, such as *Gastornis* Hébert 1855, the diatrymas, and phorusrhacids (cf. Houde, 1986; Houde and Haubold, 1987).

Saurornis matthesi Fischer 1967

Saurornis matthesi Fischer, 1967:603, pl. I.

HOLOTYPE. Distal end of coossified ulna and radius (originally described as proximal end of tarsometatarsus); GM 1956/Saur. 1.
HORIZON AND LOCALITY. Middle Eocene of Geisel Valley (5).
REMARKS. This species, originally described as avian, was later transferred to Mammalia, more specifically to the perissodactylid genus *Lophiodon* (Fischer, 1987).

Ornithoidichnites badensis Boehm 1896

Ornithoidichnites badensis Boehm, 1896:238, text-fig. 1, pl. I. *Ichnium badense:* Boehm, 1898:206 (new combination).

HOLOTYPE. Two footprints (left and right) of a single individual; location unknown. Boehm (1896) originally mentioned a series of 10 footprints, which led Brodkorb (1978:221) to consider all of them to be the holotype of *Ornithoidichnites badensis*. However, only two of these footprints were described in detail by Boehm (1896), and from his later article (Boehm, 1898), it is clear that only those two represent the holotype.
HORIZON AND LOCALITY. Upper Oligocene of Bellingen (27).
REMARKS. These footprints, originally described as avian, are actually those of a tapir (Boehm, 1898; see also Abel, 1935). Lambrecht (1933:665) and Brodkorb (1978:221) overlooked Boehm's (1898) correction and continued to list *Ornithoidichnites badensis* as avian.

Ichnoorder Avipedia Vjalov 1966

Family *incertae sedis*

Ornithotarnocia lambrechti Kordos 1983

Ornithotarnocia lambrechti Kordos, 1983:269, fig. 1.

HOLOTYPE. Two footprints (left and right) of a single individual; GIB V.12721.
HORIZON AND LOCALITY. Lower Miocene (MN 3) of Ipolytarnóc (60).
REMARKS. These footprints were first described and figured by Lambrecht (1912b, 1933).

Aviadactyla media Kordos 1983

Aviadactyla media Kordos, 1983:276, fig. 6.

HOLOTYPE. Two footprints (left and right) of a single individual; GIB V.12729.
HORIZON AND LOCALITY. Lower Miocene (MN 3) of Ipolytarnóc (60).

Tetraornithopedia tasnadii Kordos 1983

Tetraornithopedia tasnadii Kordos, 1983:279, fig. 7.

HOLOTYPE. Footprint (?left); CHI, uncatalogued.
HORIZON AND LOCALITY. Lower Miocene (MN 3) of Ipolytarnóc (60).

Passeripedia ipolyensis Kordos 1983

Passeripedia ipolyensis Kordos, 1983:280, fig. 8.

HOLOTYPE. Footprint (?right); GIB, uncatalogued.
HORIZON AND LOCALITY. Lower Miocene (MN 3) of Ipolytarnóc (60).

TERTIARY AVIAN LOCALITIES OF CENTRAL EUROPE

The following list contains all Central European localities known to me from which Tertiary birds have been recorded (Figs. 2, 3). Although no important locality appears to have been overlooked, the completeness of the list cannot be ascertained because bird finds are often just mentioned in papers on other animal groups, or even plants, and these notes are extremely difficult to detect.

The localities are listed by age. Their synonyms (in parentheses), stratigraphic and geographic position, and avian fossils recovered from each are given. The last data are, where possible, based upon revised results.

I have followed the latest administrative divisioning of the countries in describing the geographical position of the mentioned localities. I have deliberately termed the higher administrative units "districts" and the lower ones "counties"; where one-level divisioning was sufficient, the units were referred to as "provinces." The respective vernacular terms are "Land" and "Kreis" in Germany, "województwo" in Poland, "kraj" and "okres" in Czechoslovakia, "megye" in Hungary, "Land" and "Bezirk" in Austria, and "Kanton" in Switzerland. No Tertiary bird-yielding localities are known from Liechtenstein. Considerable changes in administrative divisioning of Central Europe followed both World Wars and 1989 revolutions, so many of the relevant terms applied in earlier works are outdated.

PALEOCENE

No Paleocene birds have been described from Central Europe thus far, although Walbeck (1) has yielded noticeable numbers of well-preserved avian fossils.

(1) WALBECK, Haldensleben County, Magdeburg District, Germany. Upper Paleocene (Tobien, 1986a). Numerous bird bones, including those of *Gastornis* (Weigelt, 1939, 1942).

EOCENE

Of the eight localities listed below, important avifaunal collections have come only from Messel (4) and Geisel Valley (5).

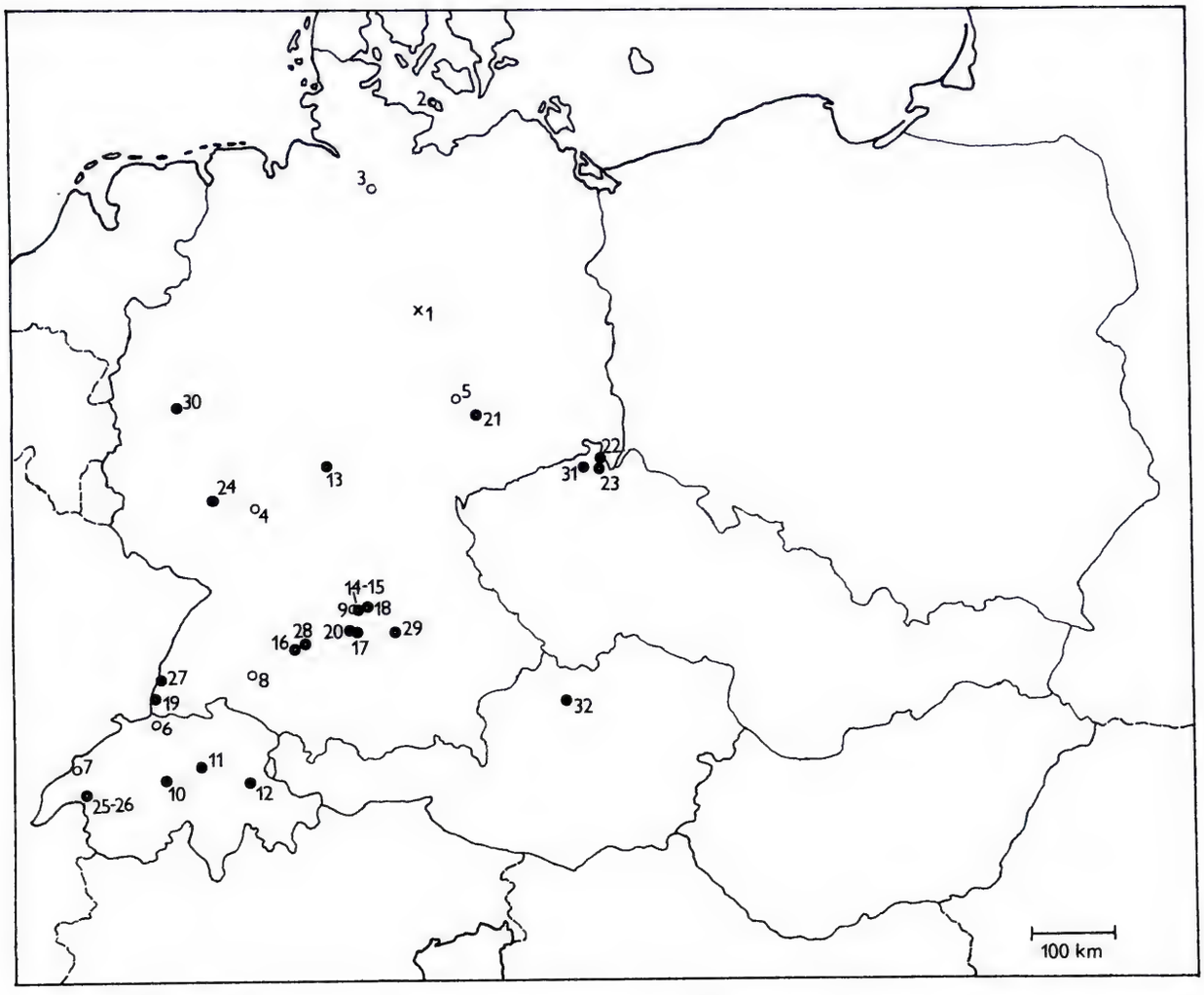

Figure 2. Map of Central Europe with distribution of its Paleogene avian localities. ×, Paleocene; ○, Eocene; ●, Oligocene. Numbering of localities agrees with that in text. Order of localities approximates their decreasing age.

(2) KATHARINENHOF, Fehmarn County, District Schleswig-Holstein, Germany. Lower Eocene (Tobien, 1986a). Three brain casts, indeterminate bird bone fragments (Hoch, 1975).

(3) HAVIGHORST (Havighorst bei Reinbek), Stormarn County, District Schleswig-Holstein, Germany. Lower Eocene (Tobien, 1986a). Feather imprints (Illies, 1941, 1942).

(4) MESSEL, Darmstadt County, District Hessen, Germany. Middle Eocene (Franzen and Haubold, 1986). Diverse avifauna, of which only a small part has been described. It includes ibises, diatrymas, messelrails, and crested swifts (Wittich, 1899; Berg, 1965; Hoch, 1980; Peters, 1983, 1985, 1987a, 1987b; Hesse, 1988). Type locality of *Juncitarsus merkeli, Rhynchaeites messelensis, Plumumida lutetialis, Messelornis cristata,* and *Aegialornis szarskii.*

(5) GEISEL VALLEY (Geiseltal), Merseburg County, Halle an der Saale District, Germany. Middle Eocene (Krumbiegel et al., 1983; Franzen and Haubold, 1986). Diverse avifauna, including palaeognathous birds, galliforms, ibises, diatrymas, flamingos, falcons, owls, swifts, and coraciiform and piciform birds. (Lambrecht, 1928, 1935; Heller, 1932; Bachofen-Echt, 1936; Fischer, 1962, 1967, 1978, 1987; Houde, 1986; Houde and Haubold, 1987; Peters, 1989). Type locality of *Saurornis matthesi, Eocathartes robustus, Diatryma geiselensis, Palaeogrus geiseltalensis, Palaeotis weigelti, Geiseloceros robustus,* and *Eoglaucidium pallas.*

(6) EGERKINGEN, Solothurn Province, Switzerland. Middle Eocene (Russell et al., 1982). Various bone fragments of a giant (?ratite) bird (Schaub, 1929, 1940a, 1940b). Type locality of *Eleutherornis helveticus.*

(7) CHAMBLON, Vaud Province, Switzerland. Middle Eocene (Russel et al., 1982). Thenius (1959) mentioned bird fossils from this locality.

(8) FROHNSTETTEN (Fronstetten), Sigmaringen County, District Baden-Württemberg, Germany. Upper Eocene (Thenius, 1959). Bird bones mentioned by Meyer (1852), Quenstedt (1853), and Lambrecht (1933:929).

(9) MÖHREN 19, Donauwörth County, District Bayern, Germany. Upper Eocene (Russell et al., 1982). Bird remains mentioned by Heissig (1978).

OLIGOCENE

Most of the 25 localities listed below are fissure fillings in the Jura Mountains of Switzerland and southwestern Germany. All

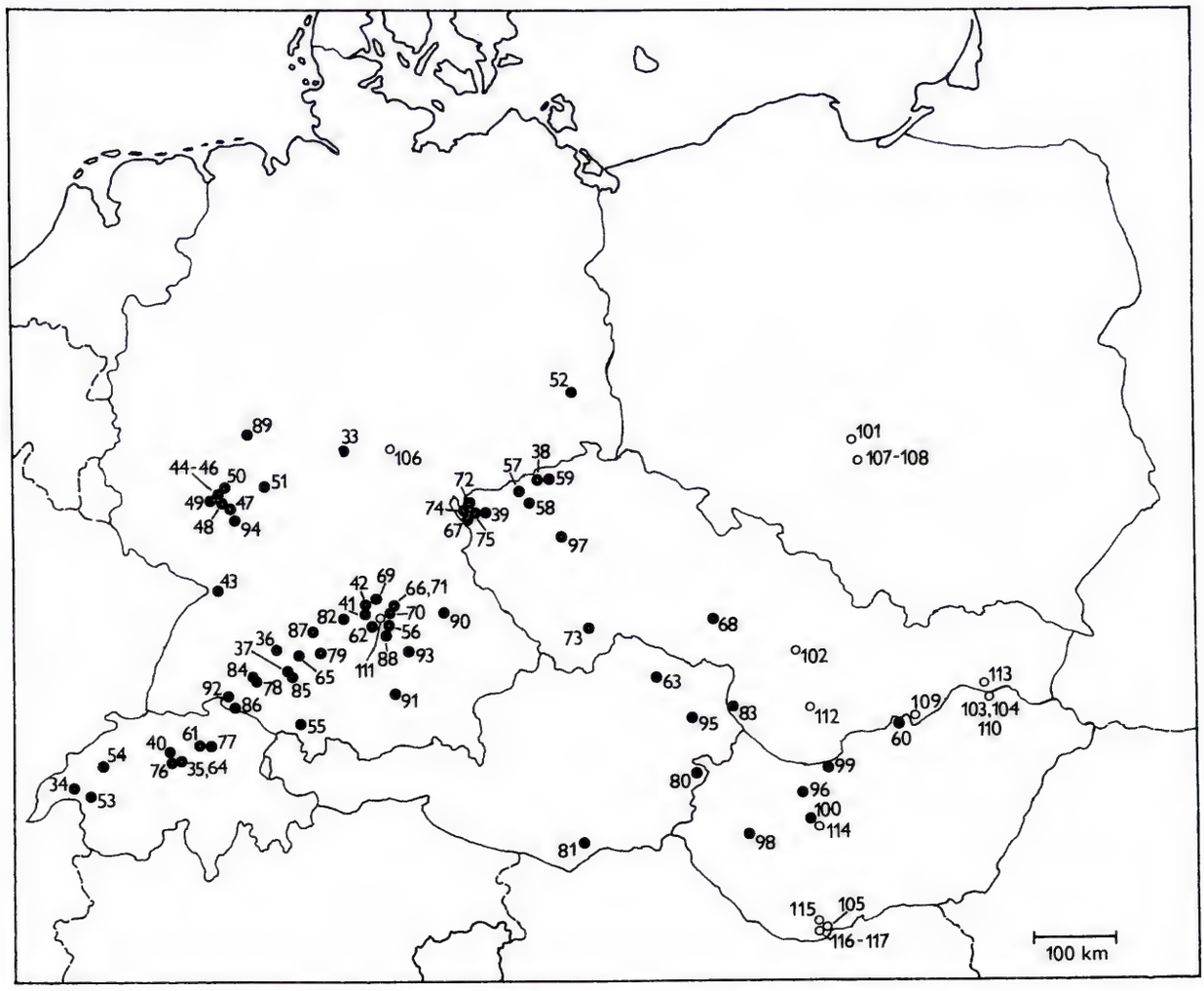

Figure 3. Map of Central Europe with distribution of its Neogene avian localities. ●, Miocene; ○, Pliocene. Numbering of localities agrees with that in text. Order of localities approximates their decreasing age.

have yielded only a few bird bones, mostly of terrestrial birds. Espenhain (21) and Traun-Pucking (32), however, have produced fossils of marine birds.

(9a) HŁUDNO, Krosno Province, Poland. Oligocene (Kotlarczyk and Jerzmańska, 1976). Leg remains of a bird, attributed to the Passeriformes (Bocheński and Szymczak, 1979).

(10) LAMMSCHLUCHT/FLÜHLI, Luzern Province, Switzerland. Lower Oligocene (cf. Weidmann and Reichel, 1979). Bird footprints, attributed to the family Rallidae (de Clercq and Holst, 1971).

(11) GOLDAU, Schwyz Province, Switzerland. Lower Oligocene (cf. Weidmann and Reichel, 1979). Bird footprints (Bräm, 1954).

(12) MATT (Engi-Matt, Engi), Glarus Province, Switzerland. Lower Oligocene (Kozur, 1984). Bones of motmots (Escher, 1839; Meyer, 1839b, 1856; Heer, 1865; Peyer, 1949, 1957; Stüssi, 1958; Baumann, 1958; Olson, 1976). Type locality of *Protornis glarniensis* and *Protornis blumeri.*

(13) SIEBLOS (Sieblos über Fulda), Fulda County, District Hessen, Germany. Lower Oligocene (Martini and Tobien, 1984). Two partial hindlimbs of birds, both probably indeterminate (Hassenkamp, 1858:207; Martini, 1967a, 1967b; Martini and Tobien, 1984). Type locality of *Pararallus hassenkampi.*

(14) MÖHREN 13, Donauwörth County, District Bayern, Germany. Lower Oligocene (Russell et al., 1982). A few bird bones mentioned by Heissig (1973).

(15) MÖHREN 6, Donauwörth County, District Bayern, Germany. Lower Oligocene (Heissig, 1970). A bird tarsometatarsus was recorded by Heissig (1970).

(16) HERRLINGEN/BLAU, Ulm County, District Baden-Württemberg, Germany. Lower Oligocene (Palmowski and Wachendorf, 1966). An ulna of a rail was noted by Immelmann (in Palmowski and Wachendorf, 1966).

(17) OPPERTSHOFEN 2, Donauwörth County, District Bayern, Germany. Lower Oligocene (Dehm, 1978). A few bones of small birds reported by Dehm (1978).

(18) WEISSENBURG 9 (Weissenburg in Bayern), Weissenburg County, District Bayern, Germany. Lower Oligocene (Dehm, 1978). Undetermined bird fossils reported by Dehm (1978).

(19) KLEINKEMS (Klein-Kems), Lörrach County, District Baden-Württemberg, Germany. Middle Oligocene (Thenius, 1959). Feather imprints (Mieg et al., 1892:379, Lambrecht, 1933: 665)

(20) BURGMAGERBEIN 3, Dillingen an der Donau County, District Bayern, Germany. Middle Oligocene (Dehm, 1978). A few bones of small birds reported by Dehm (1978).

(21) ESPENHAIN, Borna County, Leipzig District, Germany. Middle Oligocene (Fischer, 1982). Fischer (1982, 1983a, 1983b, 1985) reported a small marine avifauna. Type locality of *Diomedeoides minimus, Gaviota lipsiensis,* and *Oligostrix rupelensis.*

(22) VARNSDORF (Warnsdorf), Děčín County, District Severní Čechy, Czechoslovakia. Middle Oligocene (Konzalová, 1981; Kvaček, in litt.). Remains of an indeterminate heron (Bayer, 1882, 1883; Mlíkovský and Švec, 1989). Type locality of *Anas basaltica.*

(23) SKALICE (Skalitz), Litoměřice County, District Severní Čechy, Czechoslovakia. Middle Oligocene (Konzalová, 1981; Kvaček, in litt.). Indeterminate bird remains (Bayer, 1882, 1883; Mlíkovský and Švec, 1989). Type locality of *Anas skalicensis.*

(24) FLÖRSHEIM, Main-Taunus County, District Hessen, Germany. Upper Oligocene (Kuss, 1963). Lambrecht (1933:671) mentioned badly preserved bird remains.

(25) CHAUDERON/GRANDVAUX, Vaud Province, Switzerland. Upper Oligocene (Weidmann and Reichel, 1979). Footprints, attributed to the Rallidae and Anseridae (Weidmann and Reichel, 1979).

(26) LES ROCHES/EPESSES, Vaud Province, Switzerland. Upper Oligocene (Weidmann and Reichel, 1979). Footprints, attributed to a small wader and a ?songbird (Weidmann and Reichel, 1979).

(26a) CRAU COULET/EPESSES, Vaud Province, Switzerland. Upper Oligocene (Weidmann and Reichel, 1979). Two footprints, attributed to a wader (Weidmann and Reichel, 1979).

(27) BELLINGEN, Müllheim County, District Baden-Württemberg, Germany. Upper Oligocene (Brodkorb, 1978). No bird remains (Boehm, 1896, 1898). Type locality of *Ornithoidichnites badensis.*

(28) TOMERDINGEN, Ulm County, District Baden-Württemberg, Germany. Upper Oligocene (cf. Thenius, 1959). A bird bone, said to belong to *Palaeortyx ocyptera* Milne-Edwards 1892 (Seemann and Berckhemer, 1930; Lambrecht, 1933:671).

(29) GAIMERSHEIM, Ingolstadt County, District Bayern, Germany. Upper Oligocene (Ballmann, 1970). Ballmann (1970) reported an indeterminate turaco, family Musophagidae.

(30) ROTT, Monschau County, District Nordrhein-Westfalen, Germany. Upper Oligocene (Thenius, 1959). Feather imprints (Meyer, 1859, 1867).

(31) BECHLEJOVICE, Děčín County, District Severní Čechy, Czechoslovakia. Upper Oligocene (Č. Bůžek, pers. comm.). A feather imprint (Špinar, 1986:95, fig. 88c). The alleged bird bone from this locality illustrated by Špinar (1986:95, fig. 88d) is not bone at all (Mlíkovský, unpubl. obs.).

(32) TRAUN-PUCKING, Linz-Land County, District Oberösterreich, Austria. Upper Oligocene (J. Kovar in Mlíkovský, 1987). Partial skeleton of an auk (Mlíkovský, 1987). Type locality of *Petralca austriaca.*

MIOCENE

Miocene birds have been collected from more localities of Central Europe than all other Tertiary birds combined. Geographically, they are concentrated in the western part of Central Europe, being almost absent from its eastern part. Of the 79 localities listed here, only a few have yielded significant numbers of fossils. The complex of Aquitanian (MN 2) localities of the Mainz Basin (44–50) is completely comparable to the classic MN 2 locality of Saint-Gérand-le-Puy in France and represents the most northern and most eastern locality of the MN 2 age that has furnished a large avifauna. Of particular interest are the Early to Middle Miocene localities of the Cheb Basin (67, 71), both of which have yielded moderate freshwater avifaunas whose identification will result in the first data on avifaunal changes at the Early to Middle Miocene transition. Of the other Middle Miocene localities, Nördlinger Ries (82) is of top quality. On the other hand, all of the Late Miocene localities have yielded just a few bird bones.

In addition to the following listed localities, Meyer (1867) mentioned a feather imprint from the Miocene of Höhgau, and Lambrecht (1933:687) mentioned a bird egg from the Miocene of Heiligenstadt and a feather imprint from the Miocene of Saltzenhaufen. I was unable to identify these localities, nor verify their age, so I have excluded them from the following list.

(33) KALTENNORDHEIM (Tanne), Bad Salzungen County, Cottbus District, Germany. ?Miocene (cf. Lambrecht, 1933). Schlotheim (1820:26) reported a leg bone, said to be similar to that of *Fulica* sp.

(34) LAUSANNE, Vaud Province, Switzerland. Miocene (cf. Lambrecht, 1933). Remains of bird eggs (Gaudin, 1854).

(35) EMMENWEID, Luzern Province, Switzerland. Miocene (cf. Lambrecht, 1933). Bird eggs (Bachmann, 1878).

(36) BÖTTINGEN, Münsingen County, District Baden-Württemberg, Germany. Miocene (cf. Lambrecht, 1933). Feather imprints of a large bird, compared to those of *Aquila* sp. (Zeuner, 1931:360–61).

(37) SCHEMMERBERG, Biberbach an der Riss County, District Baden-Württemberg, Germany. Miocene (cf. Lambrecht, 1933). A few bird bones (Probst, 1879:244; Lambrecht, 1933: 681).

(38) SKYŘICE (Skiritz), Most County, District Severní Čechy, Czechoslovakia. Lower Miocene (Č. Bůžek, pers. comm.). Remains of whistling-ducks (*Mionetta* Livezey and Martin 1988) (Laube, 1910).

(39) SOKOLOV, Sokolov County, District Severní Čechy, Czechoslovakia. Lower Miocene (P. Čtyroký, pers. comm.). Indeterminate remains of a bird leg (Mlíkovský, unpubl. obs.).

(40) FISCHBACH-RÜMLING, Luzern Province, Switzerland. Lower Miocene, MN 2 (cf. Weidmann and Reichel, 1979). Footprints, attributed to waders (Gasser, 1966; Weidmann and Reichel, 1979).

(41) TREUCHTLINGEN 2, Weissenburg County, District Bayern, Germany. Lower Miocene, MN 2 (cf. Dehm, 1978). Undetermined bird remains (Dehm, 1978).

(42) WEISSENBURG 6, Weissenburg County, District Bayern, Germany. Lower Miocene, MN 2 (Schleich, 1985). Undetermined bird remains (Dehm, 1978).

(43) BÜCHELBERG, Germersheim County, District Rheinland-Pfalz, Germany. Lower Miocene, MN 2 (cf. Thenius, 1959). Bird remains, including those of *Palaelodus* (Kuss, 1960).

(44) WEISENAU (Weissenau, Mainz-Weisenau), Mainz County, District Rheinland-Pfalz, Germany. Lower Miocene, MN 2 (cf. Kuss, 1963). Remains of approximately 70 bones and 2 eggs, representing at least 12 avian species (Meyer, 1839c, 1843; Becker, 1849).

(45) BUDENHEIM, Mainz County, District Rheinland-Pfalz, Germany. Lower Miocene, MN 2 (Nordsieck, 1982). Bird remains (Lambrecht, 1933:670).

(46) OPPENHEIM, Mainz County, District Rheinland-Pfalz, Germany. Lower Miocene, MN 2 (cf. Rothausen, 1966). Bird skull, originally attributed to *Palaelodus* (Rothausen, 1966), to which it does not belong (Olson and Feduccia, 1980; Mlíkovský, 1988). Its identity remains uncertain.

(47) MOMBACH, Bernkastel County, District Rheinland-Pfalz, Germany. Lower Miocene, MN 2 (cf. Lambrecht, 1933). Bones of a "cormorant" (Hoeninghaus, 1839).

(48) INGELHEIM, Bingen County, District Rheinland-Pfalz, Germany. Lower Miocene, MN 2 (cf. Thenius, 1959). Remains of a heron (Lambrecht, 1933:670).

(49) KASTEL-BRUCH (Wiesbaden-Kastel), Wiesbaden County, District Hessen, Germany. Lower Miocene, MN 2 (cf. Thenius, 1959). Bird remains (Lambrecht, 1933).

(50) WIESBADEN, Wiesbaden County, District Hessen, Germany. Lower Miocene, MN 2 (Nordsieck, 1982). A few bird eggs and bones, including those of waterfowl and flamingos (*Palaelodus*) (Meyer, 1839c; Lambrecht, 1931, 1933; Rothausen, 1966; Eikamp, 1979). Type locality of *Cygnavus senckenbergi.*

(51) RAVOLZHAUSEN, Hanau County, District Hessen, Germany. Lower Miocene, MN 2 (cf. Martini, 1974). Small freshwater bird fauna, including cormorants, flamingos, waterfowl, waders, and hawks (Martini, 1974; Eikamp, 1980).

(52) SENFTENBERG, Senftenberg County, District Cottbus, Germany. Lower Miocene, MN 2 (cf. Lambrecht, 1933). A feather imprint (Menzel, 1906).

(53) FLON MORAND, Vaud Province, Switzerland. Lower Miocene, MN 3 (cf. Weidmann and Reichel, 1979). Footprints, attributed to Laridae and Scolopacidae (Weidmann and Reichel, 1979).

(54) LES USSEMENTS, Vaud Province, Switzerland. Lower Miocene, MN 3 (cf. Weidmann and Reichel, 1979). Footprints, attributed to Scolopacidae and Charadriidae (Weidmann and Reichel, 1979).

(54a) AUGINE 7, Vaud Province, Switzerland. Lower Miocene, MN 3 (Berger, 1985). Small avian footprints (Berger, 1985).

(54b) MAFFLON 1, Fribourg Province, Switzerland. Lower Miocene, MN 3 (Berger, 1985). Unidentified avian footprints (Berger, 1985).

(54c) LIEFFRENS 5, Fribourg Province, Switzerland. Lower Miocene, MN 3 (Berger, 1985). Unidentified avian footprints (Berger, 1985).

(54d) BRÉ 8, Fribourg Province, Switzerland. Lower Miocene, MN 3 (Berger, 1985). Avian footprints, tentatively attributed to *Lymnocryptes* (Berger, 1985).

(54e) HEITENRIED 7 (Sodbach-Heitenried), Fribourg Province, Switzerland. Lower Miocene, MN 3 (Berger, 1985). Two types of avian footprints (Berger, 1985).

(54f) BURG (Burggraben), Fribourg Province, Switzerland. Lower Miocene, MN 3 (Berger, 1985). Unidentified avian footprints (Berger, 1985).

(55) HARBATSHOFEN (Harbatzhofen), Lindau County, District Bayern, Germany. Lower Miocene, MN 3 (cf. Erb, 1923). Indeterminate bird humerus (Haushalter, 1855; Brodkorb, 1980). Type locality of *Ardeacites molassicus.*

(56) WINTERSHOF (WEST), Eichstätt County, District Bayern, Germany. Lower Miocene, MN 3 (Kretzoi, 1985). Diverse fauna of land birds, including gamefowl, hawks, owls, barbets, wood-hoopoes, zygodactylids, and many unidentified passerines (Dehm, 1937; Ballmann, 1969). Type locality of *Palaeortyx intermedia, Alectoris bavarica, Taoperdix miocaena, Otus wintershofensis, Strix brevis, Zygodactylus ignotus,* and *Capitonides europeus.*

(57) AHNÍKOV, Chomutov County, District Severní Čechy, Czechoslovakia. Lower Miocene, MN 3 (P. Čtyroký, pers. comm.). Distal end of a humerus of a ?passerine bird (Mlíkovský, unpubl. obs.).

(58) TUCHOŘICE, Louny County, District Severní Čechy, Czechoslovakia. Lower Miocene, MN 3 (O. Fejfar, pers. comm.). Two endocranial casts of an accipitrid hawk and pedal phalanges of raptors (Mlíkovský, 1980; unpubl. obs.).

(59) BŘEŠTANY (Preschen), Teplice County, District Severní Čechy, Czechoslovakia. Has not existed since 1962. Lower Miocene, MN ?3 (Č. Bůžek, pers. comm.). Small freshwater avifauna, including cormorants, herons, and storks (Laube, 1901, 1909). Type locality of *Cygnus bilinicus* and *Totanus praecursor.*

(60) IPOLYTARNÓC, Nógrád Province, Hungary. Lower Miocene, MN 3 (Kordos, 1987). Four kinds of bird footprints (Lambrecht, 1912b, 1933:675; Kordos, 1983). Type locality of *Ornithotarnocia lambrechti, Aviadactyla media, Tetraornithopedia tasnadii,* and *Passeripedia ipolyensis.*

(61) WALDHALDE/SIHL, Zug Province, Switzerland. Lower Miocene, MN 3–4 (cf. Kordos, 1983). Bird footprints, attributed to the Cursoriinae and Charadriinae (Speck, 1945).

(62) SOLNHOFEN, Weissenburg County, District Bayern, Germany. Lower Miocene, MN 3–4 (cf. Dehm, 1935). Undetermined bird bones (Dehm, 1935).

(63) LIMBERG, Hollabrun County, District Niederösterreich, Austria. Lower Miocene, MN 4 (cf. Bachmayer, 1980). Partial skeleton of *Falco* sp. (Bachmayer, 1980). Klipstein (*fide* Bonaparte, 1856:781) mentioned numerous birds from this locality.

(64) RENGGBACH, Luzern Province, Switzerland. Lower Miocene, MN 4 (cf. Weidmann and Reichel, 1979). Footprints, attributed to the Scolopacidae and Recurvirostridae (Weidmann and Reichel, 1979).

(65) KIRCHBERG, Ulm County, District Baden-Württemberg, Germany. Lower Miocene, MN 4 (cf. Cicha, 1970). A few bird bones (Probst, 1879:255; Lambrecht, 1933:681).

(66) ERKERTSHOFEN 1, Hilpoltstein County, District Bayern, Germany. Lower Miocene, MN 4 (cf. Fahlbusch, 1966). Bones of small birds (Dehm, 1978).

(67) DOLNICE, Cheb County, District Západní Čechy, Czechoslovakia. Lower Miocene, MN 4 (Fejfar and Roček, 1988). Diverse freshwater avifauna. Identified so far are loons, grebes, waterfowl, cormorants, flamingos, and gamefowl (Švec, 1980, 1981, 1982, 1983, 1984, 1985; Švec and Mlíkovský, 1986; P. Švec, pers. comm.). Type locality of *Gavia egeriana, Miobaptus walteri, Micrarallus fejfari,* and *Larus dolnicensis.* Note that records of *Querquedula, Nettion,* and *Anas* (Švec, 1981) are erroneous (Mlíkovský and Švec, unpubl. obs.).

(68) OŘECHOV, Brno-venkov County, District Jižní Morava, Czechoslovakia. Lower Miocene, MN 4 (P. Čtyroký, pers. comm.). A few bird bones (Mlíkovský, unpubl. obs.).

(69) RAITENBUCH 2, Weissenburg County, District Bayern, Germany. Lower/Middle Miocene, MN 4–5 (cf. Heissig, 1978). Bird remains (Heissig, 1978).

(70) PETERSBUCH 2, Hilpoltstein County, District Bayern, Germany. Lower/Middle Miocene, MN 4–5 (cf. Heissig, 1978). Bird remains (Heissig, 1978).

(71) ERKERTSHOFEN 2, Hilpoltstein County, District Bayern, Germany. Lower/Middle Miocene, MN 4–5 (cf. Heissig, 1978). Remains of the family Strigidae (Heissig, 1978).

(72) ZELENÁ, Cheb County, District Západní Čechy, Czechoslovakia. Lower/Middle Miocene, MN 4–5 (Č. Bůžek, pers. comm.). Two feather imprints (Mlíkovský and Švec, unpubl. obs.).

(72a) RANDECKER MAAR, Kirchheim County, District Baden-Württemberg, Germany. Middle Miocene, MN ? (Westphal, 1963; Bleich, 1988). Unidentified feather imprints and coproliths of birds (Westphal, 1963).

(73) LIŠOV, České Budějovice County, District Jižní Cechy, Czechoslovakia. Middle Miocene, MN 8 (O. Fejfar, pers. comm.). Cervical vertebra of a flamingo (Mlíkovský, unpubl. obs.).

(74) FRANTIŠKOVY LÁZNĚ, Cheb County, District Západní Čechy, Czechoslovakia. Middle Miocene, MN 5 (O. Fejfar, pers. comm.). Moderate number of bird bones, of which Dendrocygnini and flamingos (*Palaelodus*) have been identified so far (Mlíkovský, unpubl. obs.).

(75) MOKŘINA (Krottensee), Cheb County, District Západní Čechy, Czechoslovakia. Middle Miocene, MN 5 (cf. Obrhelová and Obrhel, 1984). Feather imprints (Novák, 1877:77–79, pl. II, fig. 13; pl. III, fig. 8). Novák (1877:77) mentioned that A.E. Reuss (1811–1873) had collected bird bones from this locality, but their whereabouts were already unknown in Novák's time.

(76) SULZIGTOBEL/WERTHENSTEIN, Luzern Province, Switzerland. Middle Miocene, MN 5–6 (cf. Bolliger et al., 1988; Č. Bůžek, pers. comm.). Undetermined bird footprints (Weidmann and Reichel, 1979).

(77) RISITOBEL/STÄFA, Zürich Province, Switzerland. Middle Miocene, MN 5–6 (Bolliger et al., 1988). Undetermined bird footprints (Weidmann and Reichel, 1979).

(78) HEGGBACH, Biberbach an der Riss County, District Baden-Württemberg, Germany. Middle Miocene, MN 5–6 (Zöbelein, 1983). A few bird bones (Probst, 1879:262).

(79) GÜNZBURG, Günzburg County, District Bayern, Germany. Middle Miocene, MN 5–6 (Zöbelein, 1983). Bird remains (Rühl, 1896).

(79a) PRZEWORNO 1, Walbrzych Province, Poland. Middle Miocene, MN 5–6 (Nadachowski et al., 1989). Four bones of *Miophasianus* (Bocheński, 1987).

(80) WEINGRABEN, Oberpullendorf County, District Burgenland, Austria. Middle Miocene, MN 5–6 (cf. Bachmayer, 1964). Feather imprints, attributed to grebes, ?cormorants, herons, and ducks (Bachmayer, 1964).

(81) SCHÖNWEG, Wolfsberg County, District Kärnten, Austria. Middle Miocene, MN 5–6. An egg, attributed to *Pandion* sp. (Rauscher, 1984).

(81a) ST. MARGARETHEN, St. Margarethen County, District Burgenland, Austria. Middle Miocene, MN 5–6 (O. Schultz, pers. comm.). Partial skeleton of a species of *Gavia* (Mlíkovský, unpubl. obs.).

(82) NÖRDLINGER RIES, Nördlingen County, District Bayern, Germany. Includes the following fossil bird producing sites: Adlersberg, Goldberg, Hahnenberg, Kleinsorheim (Klein-Sorheim), Lierheim, Steinberg (Spitzberg), and Wallerstein. Middle Miocene, MN 6 (Heizmann and Fahlbusch, 1983). Rich avifauna that has not yet been adequately described. Reported so far are taxa of the Pelecanidae, Ciconiidae, Phoenicopteridae, Anseridae, Rallidae, Charadriidae, Scolopacidae, Glareolidae, Psittacidae, Coliidae, Capitonidae, and Passeriformes (Fraas, 1879; Lambrecht, 1933:677; Seemann, 1941; Ballmann, 1979, 1983; Heizmann and Fahlbusch, 1983; Mlíkovský, 1988). Type locality of *Pelecanus intermedius, Pelecanus fraasi, Anas risgoviensis, Mioglareola gregaria, Glareola neogaena,* and *Capitonides protractus.*

(83) DĚVÍNSKÁ NOVÁ VES (Neudorf), Bratislava County, Bratislava District, Czechoslovakia. Middle Miocene, MN 6 (Kordos, 1987). Švec (1986) described from this locality two bone fragments of *Miophasianus,* but a larger number of bird bones are known from this site (Thenius, 1959:85; H. Zapfe *fide* O. Schultz, in litt., 1988; Mlíkovský, unpubl. obs.).

(84) STORZINGEN (not Stotzingen, as written in Lambrecht, 1933), Sigmaringen County, District Baden-Württemberg, Germany. Middle Miocene, MN 6–7 (cf. Probst, 1879). A few bird bones (Probst, 1879:244).

(85) BALTRINGEN, Biberbach an der Riss County, District Baden-Württemberg, Germany. Middle Miocene, MN 6–7 (cf. Probst, 1879). A few bird bones (Probst, 1879:244).

(86) ÖHNINGEN (Oehningen, Öningen, Oeningen, Steyn, Stein, Stein am Rhein), Konstanz County, District Baden-Württemberg, Germany. Middle Miocene, MN 7 (Tobien, 1986b). Only waterfowl and gamefowl (indet.) have been mentioned from this locality so far, but more avian fossils from this site are apparently scattered over various central and western European museums (Scheuchzer, 1708; Karg, 1805; Meyer, 1838, 1839a, 1845, 1864, 1865; Heer, 1865:408). Type locality of *Anas oeningensis* and *Anas meyerii.*

(87) STEINHEIM (Steinheim am Albuch), Heidenheim an der Brenz County, District Baden-Württemberg, Germany. Middle Miocene, MN 7 (Jung and Mayr, 1980). Small, mainly freshwater avifauna, including pelicans, waterfowl, ibises, flamingos, rails, bustards, and gamefowl (Fraas, 1870, 1879; Lydekker, 1891; Lambrecht, 1933:677–78). Type locality of *Ardea similis, Palaelodus steinheimensis, Anas atava, Anas cygniformis,* and *Otis affinis.*

(88) ATTENFELD, Neuburg an der Donau County, District Bayern, Germany. Middle Miocene, MN 7 (cf. Thenius, 1959). Small avifauna, including waterfowl, gamefowl, and passerines (Lambrecht, 1933:687).

(89) CLIMBACH 1, Giessen County, District Hessen, Germany. Middle Miocene, MN 7 (cf. Thenius, 1959). Dieffenbach (1853:685) mentioned "many bird bones" from this locality (see also Engelhardt and Schottler, 1914:328).

(90) DECHBETTEN, Regensburg County, District Bayern, Germany. Middle Miocene, MN 7–8 (cf. Steininger et al., 1987). Small avifauna, including cormorants and gamefowl (Ammon, 1918). Type locality of *Phalacrocorax praecarbo, Botaurites avitus, Ardea brunhuberi, Phasianus augustus,* and *Gallus longaevus.*

(91) AUMEISTER, München County, District Bayern, Germany. Middle/Upper Miocene, MN 8–9 (O. Fejfar, pers. comm.). Small freshwater avifauna, including herons and waterfowl (Stromer, 1928:4; Lambrecht, 1933). Type locality of *Anas isarensis.*

(92) HÖWENEGG, Donaueschingen County, District Baden-Württemberg, Germany. Upper Miocene, MN 9 (Tobien, 1986b). A bird bone (Jörg, 1957:120).

(93) SANDELZHAUSEN, Mainburg County, District Bayern, Germany. Upper Miocene, MN ?9 (cf. Fahlbusch and Gall, 1970). Bird bones (Fahlbusch and Gall, 1970).

(94) EPPELSHEIM, Alzey County, District Rheinland-Pfalz, Germany. Upper Miocene, MN 9 (Fejfar and Heinrich, 1987). A duck and a crane were recorded from here (Lambrecht, 1933), but both records are doubtful. Type locality of *Anas eppelsheimensis* and *Pliogrus germanicus.*

(95) VÖSENDORF (Brunn-Vösendorf), Mödling County, District Niederösterreich, Austria. Upper Miocene, MN 10 (Steininger et al., 1987). Two bird bones, including one of *Palaeocryptonyx* sp. (Thenius, 1954).

(96) CSÁKVÁR, Fejér Province, Hungary. Upper Miocene, MN 10 (Fejfar and Heinrich, 1987). Small avifauna, including swans, cranes, and owls (Lambrecht, 1929; Kretzoi, 1957). Type locality of *Cygnus csakvarensis* and *Bubo florianae.*

(96a) GÖTZENDORF (Götzendorf an der Leitha, Mannersdorf), Mannersdorf am Leithagebirge County, District Nierderösterreich, Austria. Upper Miocene, MN 10 (Bachmayer and

Wilson, 1984; Rabeder, 1989) or MN 11 (cf. Lueger, 1981). Small freshwater avifauna, including *Anhinga* and *Dendronessa* (Mlíkovský, 1991).

(97) SUCHOMASTY 3, Beroun County, District Střední Čechy, Czechoslovakia. Upper Miocene, MN 11 (I. Horáček, pers. comm.). A few bird bones (Mlíkovský, unpubl. obs.).

(98) SÜMEG, Veszprém Province, Hungary. Upper Miocene, MN 11 (Kordos, 1987) or MN 12 (Fejfar and Heinrich, 1987). A few bird bones, including those of *Palaeortyx* and a swift (?*Chaetura*) (Jánossy, 1976b, 1977). Type locality of *Chaetura baconica.*

(99) TARDOSBÁNYA, Komárom Province, Hungary. Upper Miocene, MN 12 (Kordos, 1987). Bones of *Palaeortyx* (Jánossy, 1976b).

(100) POLGÁRDI, Fejér Province, Hungary. Upper Miocene, MN 13 (Fejfar and Heinrich, 1987; Kordos, 1987). Moderate number of bird bones, including those of gamefowl, bustards, rails, waders, owls, and passerines (Lambrecht, 1912b; Jánossy, 1976b, 1979). Type locality of *Anas albae.*

PLIOCENE

None of the 19 localities listed below has yielded significant numbers of bird bones except Rębielice Królewskie 1 (107) and Villány 3 (115). The Pliocene localities are concentrated in the eastern part of Central Europe, the opposite of the Miocene localities.

(101) WĘŻE 1, Sieradz Province, Poland. Lower Pliocene, MN 15 (Fejfar and Heinrich, 1987). Small avifauna, comprising gamefowl only (Jánossy, 1974b). Type locality of *Tetrao conjugens* and *Francolinus capeki wenzensis.*

(102) IVANOVCE, Trenčín County, District Západné Slovensko, Czechoslovakia. Lower Pliocene, MN 15 (Fejfar and Heinrich, 1985). Bone remains of undetermined passerines (P. Švec in Fejfar and Heinrich, 1985).

(103) OSZTRAMOS 1 (Estramos), Borsod-Abaúj-Zemplén Province, Hungary. Lower Pliocene, MN 15 (cf. Jánossy, 1986). A few bird bones (Jánossy, 1976b, 1979). Type locality of *Turdoides borealis.*

(104) OSZTRAMOS 9 (Estramos), Borsod-Abaúj-Zemplén Province, Hungary. Lower Pliocene, MN 15 (cf. Fejfar and Heinrich, 1983). Type locality of *Porzana estramosi* (Jánossy, 1979).

(105) CSARNÓTA 2, Baranya Province, Hungary. Lower Pliocene, MN 15 (Fejfar and Heinrich, 1987). Moderate avifauna, including gamefowl, rails, waders, cuckoos, owls, and passerines (Jánossy, 1976a, 1976b, 1977). Type locality of *Tetrao macropus, Scolopax baranensis, Gallinago veterior,* and *Cuculus csarnotanus.*

(105a) GUNDERSHEIM, Worms County, District Rheinhessen, Germany. Lower Pliocene, MN 15? (I. Horáček, pers. comm.). A carpometacarpus, attributed to *Turdus* sp. (Heller, 1936).

(106) RIPPERSRODA 1, Arnstadt County, Erfurt District, Germany. Middle Pliocene, MN 15–16 (O. Fejfar, pers. comm.; see also Mai et al., 1963; Velitzelos and Gregor, 1987). Fossils of an eagle-owl and passerines (Giebel, 1860). Type locality of *Ardea lignitum.*

(107) RĘBIELICE KRÓLEWSKIE 1, Częstochowa Province, Poland. Upper Pliocene, MN 16 (Fejfar and Heinrich, 1987). Diverse avifauna, including gamefowl, owls, hawks, cranes, waders, and passerines (Jánossy, 1974b). Type locality of *Lagopus lagopus atavus, Francolinus capeki villanyiensis,* and *Athene noctua veta.*

(108) RĘBIELICE KRÓLEWSKIE 2, Częstochowa Province, Poland. Upper Pliocene, MN 16 (Fejfar and Heinrich, 1987). Only gamefowl recorded so far (Jánossy, 1974b). Type locality of *Francolinus minor.*

(109) HAJNÁČKA (Ajnácskö), Rimavská Sobota County, District Východné Slovensko, Czechoslovakia. Upper Pliocene, MN 16 (Fejfar and Heinrich, 1985). Fossils of waterfowl (*Mergus* sp.) (P. Švec in Fejfar and Heinrich, 1985).

(110) OSZTRAMOS 7 (Estramos), Borsod-Abaúj-Zemplén Province, Hungary. Upper Pliocene, MN 16 (Fejfar and Heinrich, 1987). Small terrestrial avifauna, including gamefowl and owls (Jánossy, 1976b, 1977, 1986).

(111) SCHERNFELD, Eichstätt County, District Bayern, Germany. Upper Pliocene, MN 17 (Fejfar and Heinrich, 1985). Undetermined bird bones (Dehm, 1962).

(111a) KIELNIKI 3B, Częstochowa Province, Poland. Upper Pliocene, MN 17 (Nadachowski et al., 1989). A single bone of *Lagopus* (Bocheński, 1989).

(112) KOLÍŇANY 2, Nitra County, District Západné Slovensko, Czechoslovakia. Upper Pliocene, MN 17 (I. Horáček, pers. comm.). A few bird bones (Mlíkovský, unpubl. obs.).

(113) VČELÁRE 3 (Méhész), Košice-vidiek County, District Východné Slovensko, Czechoslovakia. Upper Pliocene, MN 17 (Horáček, 1985). A few bird bones (Horáček, 1985).

(114) KISLÁNG, Fejér Province, Hungary. Upper Pliocene, MN 17 (cf. Jánossy, 1986). A few bird bones, including those of *Struthio* sp. and *Anas* (Kretzoi, 1954, 1955; Jánossy, 1986). Type locality of *Struthio pannonicus.*

(115) VILLÁNY 3, Baranya Province, Hungary. Upper Pliocene, MN 17 (cf. Jánossy, 1986). Moderate-sized avifauna, including grebes, waterfowl, gamefowl, bustards, hawks, owls, pigeons, woodpeckers, and passerines (Jánossy, 1976a, 1976b, 1977, 1979, 1980; Mlíkovský, 1981, 1982). Type locality of *Anas submajor, Francolinus subfrancolinus, Surnia robusta,* and *Dendrocopos praemedius.*

(116) BEREMEND 5, Baranya Province, Hungary. Upper Pliocene, MN 17 (cf. Jánossy, 1986). Small avifauna, including gamefowl, rails, swifts, and passerines (Jánossy, 1976b, 1977). Type locality of *Gallus beremendensis.*

(117) BEREMEND 11, Baranya Province, Hungary. Upper Pliocene, MN 17 (cf. Jánossy, 1986). A few bird bones, including those of *Francolinus* sp., *Falco* sp., and undetermined passerines (Jánossy, 1986).

SUMMARY

A review of the present state of knowledge of the Tertiary birds of Central Europe shows that fossils of Tertiary birds are known from at least 132 localities within the region. These localities range in age from the Late Paleocene to the latest Pliocene. Fossil birds have been adequately described from just a few of these localities. The most important localities appear to be Walbeck (Late Paleocene), Messel (Middle Eocene), Wintershof-West (MN 3), Dolnice (MN 4), Nördlinger Ries (MN 6), Polgárdi (MN 13), Rębielice Królewskie 1 (MN 16), and Villány 3 (MN 17). Best documented are the Early and Middle Miocene birds of Central Europe.

At least 94 species group names were first given to the Tertiary birds of Central Europe, of which six are *nomina nuda,* 2 are based upon non-avian material, 21 were shown to be misidentified as to the family within the class Aves, 9 were shown to

be misidentified as to the genus within families, 1 was synonymized within genus, and 13 are to be currently regarded as having uncertain taxonomic position. Forty-eight, or 54 percent, of these species group names were not listed in Brodkorb's catalogue of fossil birds (Brodkorb, 1963, 1964, 1967, 1971, 1978). Data on the original description, holotypes, and their location (if known) and the age and locality from which each species or subspecies was found are given. The data for the taxa listed in Brodkorb's catalogues were checked, corrected in some cases, and sometimes supplemented.

At least 32 genus group names were first given to the Tertiary birds of Central Europe, of which 2 are *nomina nuda,* 10 were shown to be misclassified as to the family, 1 was synonymized within family, and 4 are to be currently regarded as having uncertain taxonomic position. Eighteen, or 56 percent, of these genus group names were not listed in Brodkorb's catalogue of fossil birds.

New taxonomic conclusions are as follows: (1) *Cygnus csakvarensis* belongs in the genus *Olor;* (2) *Anas isarensis* is an indeterminate member of the tribe Aythyini; (3) *Anas atava* belongs in the genus *Cygnus;* (4) *Anas eppelsheimensis* is Anseridae *incertae sedis;* (5) *Athene noctua veta* is synonymous with the modern *Aegolius funereus;* (6) *Ardea lignitum* is synonymous with the modern *Bubo bubo;* and (7) *Eleutherornis helveticus, Anas risgoviensis, Anas meyerii, Totanus praecursor, Scolopax baranensis, Gallinago veterior,* and *Turdoides borealis* should be considered Aves *incertae sedis* until their types are restudied.

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APPENDIX 1

List of family group names based upon Tertiary birds of Central Europe. Type genera are given in parentheses and the original taxonomic level is indicated.

Capitonididae Prum 1988 (*Capitonides* Ballmann 1969)—family.
Diomedeoididae Fischer 1985 (*Diomedeoides* Fischer 1985)—family.
Eleutherornithidae Wetmore 1951 (*Eleutherornis* Schaub 1940)—family.
Messelornithidae Hesse 1988 (*Messelornis* Hesse 1988)—family.
Palaeotididae Houde and Haubold 1987 (*Palaeotis* Lambrecht 1928)—subfamily.
Petralcidae Mlíkovský 1987 (*Petralca* Mlíkovský 1987)—subfamily.
Zygodactylidae Brodkorb 1971 (*Zygodactylus* Ballmann 1969)—family.

APPENDIX 2

List of genus group names based upon Tertiary birds of Central Europe. Type species are given in parentheses.

Aenigmavis Peters 1987 (*Aenigmavis sapea* Peters 1987).
Ardeacites Haushalter 1855 (*Ardeacites molassicus* Haushalter 1855).
Aviadactyla Kordos 1983 (*Aviadactyla media* Kordos 1983)—ichnogenus.
Botaurites Ammon 1918 (*Botaurites avitus* Ammon 1918 =*Graculus intermedius* Milne-Edwards 1867).
Capitonides Ballmann 1969 (*Capitonides europeus* Ballmann 1969).
Cygnanser Kretzoi 1957 (*Cygnus csakvarensis* Lambrecht 1933).
Cygnavus Lambrecht 1931 (*Cygnavus senckenbergi* Lambrecht 1931).
Diomedeoides Fischer 1985 (*Diomedeoides minimus* Fischer 1985).
Eleutherornis Schaub 1940 (*Eleutherornis helveticus* Schaub 1940).
Eocathartes Lambrecht 1935 (*Eocathartes robustus* Lambrecht 1935).
Eoglaucidium Fischer 1987 (*Eoglaucidium pallas* Fischer 1987).
Geiseloceros Lambrecht 1935 (*Geiseloceros robustus* Lambrecht 1935).
Lambrechtia Jánossy 1974. [Type species neither designated nor indicated, hence a *nomen nudum* according to provisions of Article 13b of the International Code of Zoological Nomenclature (ICZN, 1985).]
Messelornis Hesse 1988 (*Messelornis cristata* Hesse 1988).
Microrallus Švec 1983 (*Microrallus fejfari* Švec 1983).
Miobaptus Švec 1982 (*Miobaptus walteri* Švec 1983).
Miogallus Lambrecht 1933 (*Gallus longaevus* Ammon 1918).
Mioglareola Ballmann 1979 (*Mioglareola gregaria* Ballmann 1979).
Oligostrix Fischer 1982 (*Oligostrix rupeliensis* Fischer 1982 =*nomen nudum*)—*nomen nudum.*
Oligostrix Fischer 1983 (*Oligostrix rupelensis* Fischer 1983).
Ornithotarnocia Kordos 1983 (*Ornithotarnocia lambrechti* Kordos 1983)—ichnogenus.
Osteornis Gervais 1844 (*Osteornis scolopacinus* Gervais 1844 =*nomen nudum*)—*nomen nudum.*
Pachystruthio Kretzoi 1954 (*Struthio pannonicus* Kretzoi 1954 =*Struthiolithus chersonensis* Brandt 1873).
Palaeogrus Lambrecht 1935 (*Palaeogrus geiseltalensis* Lambrecht 1935).
Palaeotis Lambrecht 1928 (*Palaeotis weigelti* Lambrecht 1928).
Passeripedia Kordos 1983 (*Passeripedia ipolyensis* Kordos 1983)—ichnogenus.
Petralca Mlíkovský 1987 (*Petralca austriaca* Mlíkovský 1987).
Pliogrus Lambrecht 1933 (*Pliogrus germanicus* Lambrecht 1933).
Plumumida Hoch 1980 (*Plumumida lutetialis* Hoch 1980 =*Rhynchaeites messelensis* Wittich 1899).
Protornis Meyer 1844 (*Protornis glarniensis* Meyer 1844).
Rhynchaeites Wittich 1899 (*Rhynchaeites messelensis* Wittich 1899).
Tetraornithopedia Kordos 1983 (*Tetraornithopedia tasnadii* Kordos 1983)—ichnogenus.
Zygodactylus Ballmann 1969 (*Zygodactylus ignotus* Ballmann 1969).

PALEORNITHOLOGICAL STUDIES IN BULGARIA

Zlatozar N. Boev

ABSTRACT. A review of the current state of paleornithological research in Bulgaria reveals that little work has been done in the field to date. Discoveries of avian fossils in Bulgaria have been incidental to other research, and the specimens have usually not been studied. Summary data on avian fossils reported from Bulgaria, their age, and the level to which they have been researched are given. At present, paleornithological research in Bulgaria can only be carried out in collaboration with specialists from other countries.

Key words: Bulgaria, Aves, fossil birds.

INTRODUCTION

Bulgaria is positioned as a crossroads in Southeastern Europe, and much of the country served as a natural bridge for the interchange of the terrestrial faunas of Europe, Asia, and Africa during the last 50 million years. The geological history of the country, its exceptionally varied relief, which hosts a well-expressed vertical zonality, and its role in faunal interchange are the principal factors that have determined the uniqueness of its Recent avifauna.

This review summarizes the data currently available on the paleoavifauna of Bulgaria.

GEOLOGICAL HISTORY AND ECOSYSTEM STATUS IN BULGARIA

The territory of the Balkan Peninsula, including Bulgaria, has a very complex geological history. Two marine transgressions and regressions during the Jurassic affected almost the entire country, with only part of southern Bulgaria remaining above the seas. The main bodies of the Middle and Eastern Stara Planina (Balkan) Mountains formed in the Early Cretaceous. Together with the Rila-Rhodope Mountain Massif they formed a land mass (Nikolov and Christchev, 1973). Southeastern Bulgaria and much of the Balkans were flooded by the sea near the end of the Cretaceous (Natchev and Sapunov, 1973; Bonchev, 1981), as was the northern part of the country. The Sredna Gora (Anti-Balkan), Rila, and Rhodopes Mountains remained as dry land.

Paleocene deposits appear mainly in the foothills of the Balkan ranges, whereas Eocene sediments crop out in northern Bulgaria, the Rhodope Mountains, and the Sredna Gora Mountains (Bonchev et al., 1973). Large freshwater lakes appeared in the Upper Eocene in western Bulgaria. At the same time, a large part of eastern and southeastern Bulgaria was flooded by the Euxinian Sea, which formed a complex system of bays and peninsulas. In the Miocene, the northeastern part of the country was covered by a large embayment of the Crimea–Caucasian Sea, while waters of the Central Parathetys Sea covered northwestern Bulgaria. Miocene deposits are thus widespread in northern Bulgaria.

During the Pliocene, large freshwater lakes appeared in the valleys of southern Bulgaria (Popov, 1973). Deposits from this period have been found in Dobrudja, Ludogorije, near the towns of Lom and Sofia, and the Struma, Mesta, Tundja, Maritza, and Iskar River valleys (Bonchev et al., 1973). A warm and humid climate prevailed as the principal modern mountain chains developed. This changed with the onset of the Pleistocene, which saw the formation of glaciers in the higher parts of the Rila and Pirin Mountains, glaciers that reached down to 1,110–900 m above sea level. Pleistocene fluvial sediments are found scattered across the country and thick layers (30–40 m) of loess formed in northern Bulgaria.

During the Holocene, about 90 percent of Bulgaria appears to have been covered by forests, with the remainder comprising steppe regions in the northeast, swamps, lakes, and treeless high-altitude zones. At present, 27 percent of the country is woodland and 14 percent is grassland (Bondev, 1986). Almost half of these habitats have been altered by human activity.

Five types of vegetation are present in the modern flora of Bulgaria: arctoalpine, boreomontane, nemoral, steppe, and Mediterranean and sub-Mediterranean. All lowlands and plains, including the Danubian Plain, South Dobrudja, the Upper Thracian Plain, and the Tundja Valley, are agricultural lands. The oak zone in all mountains has been virtually destroyed over the last 200 years.

Eurosiberian, mid-European, arctoalpine, steppe, pontic, sub-Mediterranean, and Mediterranean zoogeographic elements are presented in the terrestrial fauna of Bulgaria (Popov and Kumansky, 1981). The Recent vertebrate fauna includes about 690 species, although 143 of them are very rare or endangered. Fifteen other species have disappeared from the wild in Bulgaria over the last 40 years (*Red Data Book of Bulgaria*, 1985). With few exceptions, all freshwater lakes in the country have been drained, and Black Sea saltwater lakes have been turned into

reservoirs, salt-farming basins, or basins for industrial waste or put to other unnatural uses. Protected natural areas account for only 1 percent of the country, and include 7 national parks and about 100 small nature reserves. Most are affected by various human activities.

PRESENT STATE OF RESEARCH ON THE RECENT AVIFAUNA OF BULGARIA

In Bulgaria, a relatively small territory of 111,000 km², a total of 376 species of resident, migratory, and vagrant bird species have been recorded. Those breeding regularly or occasionally in the country number 256 species. Two of the five principal migration routes for European species that winter in Africa and the Near East pass through Bulgaria, and it is home to wintering populations of many Middle European, East European, and some West Siberian populations.

Until 1950, the number of bird species recorded for Bulgaria was 341 (Patev, 1950). This number has increased to 354 by 1982, and during the last decade at least one new species has been recorded for the country annually. Activity in avian research is currently high and the number of interested persons is increasing rapidly. The Bulgarian Society for Protection of Birds was founded in 1988, although the Bulgarian Banding Center has successfully carried out its work for more than 60 years, with approximately 300,000 birds having been banded to date. The *Bulgarian Red Data Book* on animals was published in 1985, and data on the number and distribution of 100 rare bird species are included in it. The first volume of a projected three-volume series on the Bulgarian avifauna is in press.

STATE OF PALEORNITHOLOGICAL RESEARCH IN BULGARIA

Very few data have been published on the origins or paleobiogeography of the Bulgarian avifauna. Most avian fossils in the country have been found by chance at mine excavations, at drilling sites, or at paleontological or archaeological sites. No special attention has been paid to these avian fossils, partly owing to the absence of researchers in paleornithology. Although researchers of other countries have worked on material from various sites in neighboring Balkan countries, Bulgaria has remained beyond their attention.

The primary problem at present is the lack of comparative osteological collections of modern birds. The Ornithological Section of the National Museum of Natural History began building an osteological collection in 1981, which by the end of October 1991 consisted of more than 1300 skeletons of about 274 species, mostly of European species. Small collections of skeletons are in the Yambol District Museum, Yambol (150 specimens, 70 species), and the Faculty of Biology, University of Sofia (50 specimens, 40 species). Another serious problem is the difficult access to foreign paleontological literature.

Work by foreign specialists suggest that paleornithology is a highly promising field in Bulgaria. For example, Burchak-Abramovich and Nikolov (1984) have described two new Miocene bird species, and Bocheński (1982) identified two Pleistocene species that are now absent from the Bulgarian avifauna. Within Bulgaria, information on paleornithological and archaeological studies has been increasingly sought and valued, suggesting a strong future. Several papers, cited later, have been published on archaeological excavations. A complete list of all paleornithological sites in Bulgaria, accurate through August 1988 follows. The sites are mapped in Fig. 1. If no reference is given for the information presented, it reflects my observations.

Materials from sites 1, 2, 4, 5, 7, 21, 35, and 36 are housed at the National Museum of Natural History, Bulgarian Academy of Sciences, while materials from localities 11, 12, 16–20, and 37–40 are housed at the Institute of Zoology, Bulgarian Academy of Sciences. Part of the material from localities 3, 8–15, and 23–33 is housed at the Archaeological Institute and Museum, Bulgarian Academy of Sciences. Material from locality 22 is kept at the Higher Institute of Agronomy, Stara Zagora.

MIOCENE

(1) Kardam

An almost complete skeleton of a thrush-sized song bird was found in clay deposits at a depth of 102 m during drilling operations sometime c. 1950–1955. The specimen is under study.

(2) Hrabarsko (Pontian)

Phlacrocorax serdicensis Burchak-Abramovich and Nikolov (1984): fragments of humerus, scapula, coracoid, carpometacarpus, ulna, sternum, and three thoracic vertebrae. An almost complete skeleton of a charadriiform bird, the size of *Larus ridibundus* Linnaeus 1766, the Black-headed Gull, was found fossilized in tar in 1955. The specimen is under study.

(3) Sofia (Pontian)

Unknown number of unidentified bones (Popov et al., 1921).

(4) Troyanovo Mine (Pontian)

Anser thraceiensis Burchak-Abramovich and Nikolov (1984): fragments of humerus, coracoid, scapula, ulna, radius, carpometacarpus, os unciform, and sternum.

PLIOCENE

(5) Dorkovo (Ruscinian)

Tetraoninae gen. et sp.: distal epiphysis of humerus; found in 1986. Anatidae gen. et sp., distal end of humerus and cf. Coraciiformes, part of distal epiphysis of tibiotarsus. Both of the latter specimens were found in 1987; they are under study.

PLEISTOCENE

(6) Bacho Kiro Cave (Paleolithic)

Popov (1911, 1912) reported unidentified bird bones from this site. Bocheński (1982) later reported on 87 specimens, 68 of which were identified as belonging to 21 species: *Anas platyrhynchos* Linnaeus 1758, *Aquila chrysaetos* (Linnaeus 1758), *Circus aeruginosus* (Linnaeus 1758), *Lagopus mutus* (Montin 1776), *Perdix perdix* (Linnaeus 1758), *Alectoris graeca* (Meisner 1804), *Rallus aquaticus* Linnaeus 1758, *Porzana porzana* Linnaeus 1766, *Gallinula chloropus* (Linnaeus 1758), *Bubo bubo* (Linnaeus 1758), *Ptyonoprogne rupestris* (Scopoli 1769), *Delichon urbica* (Linnaeus 1758), *Lullula arborea* (Linnaeus 1758), *Alauda arvensis* Linnaeus 1758, *Anthus campestris* (Linnaeus 1758), *Pyrrhocorax pyrrhocorax* (Linnaeus 1758), *P. graculus* (Linnaeus 1766), *Corvus monedula* Linnaeus 1758, *C. corax* Linnaeus 1758, *Turdus philomelos* Brehm 1831, and *Loxia curvirostra* Linnaeus 1758.

(7) Varchets

Perdix perdix, Pyrrhocorax graculus, and other unidentifiable small bone fragments were found in 1987. [Note added in press: This locality is now referred to the upper Pleistocene.]

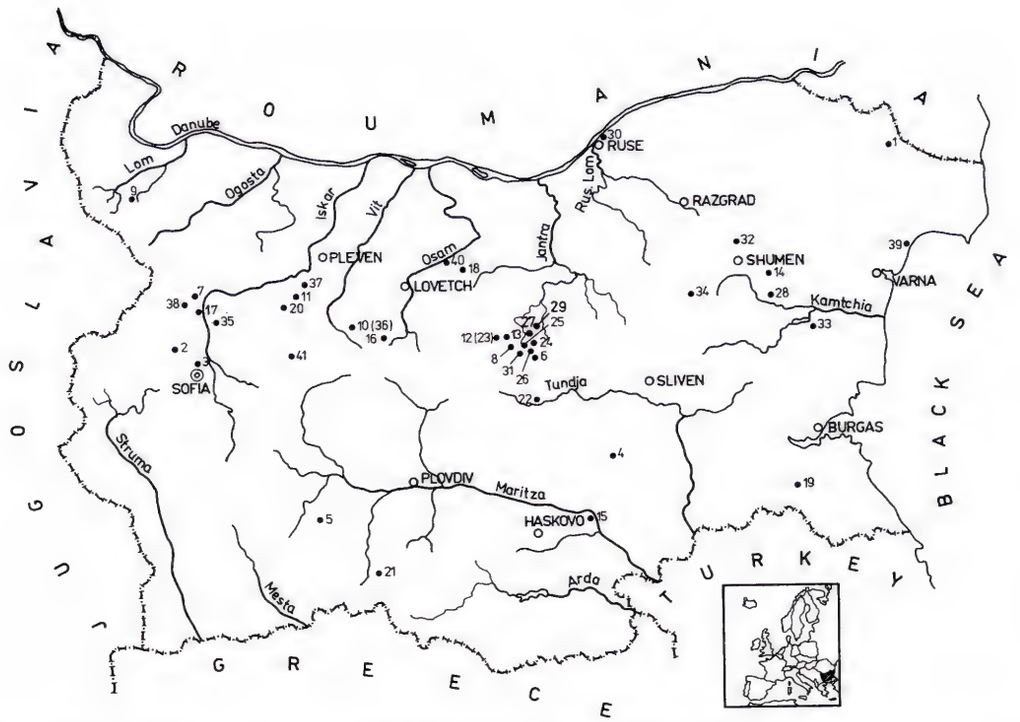

Figure 1. Locations of fossil bird sites in Bulgaria. The numbers on the map correspond to those in the text.

(8) Malkata Podlizha Cave (Paleolithic)

Unidentified bird remains (Popov, 1913a, 1925).

(9) Mirizlivka Cave (Paleolithic)

Popov (1933) reported a bird metacarpus and a radius from this site.

(10) Morovitsa Cave (Paleolithic)

Popov (1913b, 1920) reported unidentified bird bones from this cave. In 1982, 30 identifiable specimens were collected in this cave.

(11) Temnata Dupka Cave (Paleolithic)

Popov (1931b) reported an unknown number of unidentified bird bones from this site, and later (Popov, 1931a:128, fig. 62) a femur. It is clear from the figure that this femur belongs to a hare (*Lepus europaeus* Pallas 1778). Ten identifiable specimens were collected here in 1982. New material collected in 1988–1991 belongs to at least 29 Recent species.

(12) Golyamata Peshtera Cave (Paleolithic)

Popov (1904:11) reported an unidentified ulna, femur, and two humeri as well as a tarsometatarsus identified as "*Aquila/Pandion.*"

(13) Golyama Listsa Cave (Paleolithic)

Popov (1904) reported unidentified bird bones from here.

(14) Madara (Paleolithic)

Popov (1904) reported an unidentified bird humerus and femur.

(15) Deve-Bargan Mound (Paleolithic)

Popov (1926:82, fig. 140) reported an unidentified tibiotarsus, possibly from a charadriiform.

UPPER PLEISTOCENE

A total of 126 identifiable bird specimens were collected from the following five caves in the years 1982–1985.

(16) Toplya Cave

(17) Kozarska Cave

(18) Gornik Cave

(19) Metcha Dupka Cave (Strandja Mountain)

(20) Cave No. 16

HOLOCENE

(21) Orpheus Chalet (Rock Crevice)

Cf. *Turdus ruficollis* Pallas 1776, a synsacrum.

(22) Kazanluk (Neolithic Mound)

Boev (1988) reported a humerus and two synsacra of *Tetrao tetrix* Linnaeus 1758. *Pelecanus crispus* Bruch 1832, *Perdix perdix, Aquila chrysaetos,* cf. *Otis tarda* Linnaeus 1758, and cf. *Phasianus colchicus* Linnaeus 1758 have also been identified from the mound, but not yet published. Dennel (1978) reported nine unidentified bird bones from the site.

(23) Golymata Peshtera Cave (Neolithic)

Popov (1925) reported unidentified bird bones.

(24) Tsarskata Peshtera Cave (Neolithic)

Popov (1925) reported unidentified bird bones.

(25) Malka Listsa Cave (Neolithic)

Popov (1911, 1912, 1925) reported unidentified bird bones.

(26) Popin Ptchelin Cave (Neolithic)

Popov (1925) reported unidentified bird bones.

(27) Golyama Listsa Cave (Neolithic)

Popov (1921b, 1925) reported unidentified bird bones.

(28) Deneva Mound (Neolithic/Chalcolithic)

Popov (1915:206) reported unidentified bird bones.

(29) Derventska Mound

Popov (1908) reported an unknown number of bird bones.

(30) Ruse (Neolithic Mound)

Popov (1921a, 1921c) reported unidentified bird bones, but no additional specimens were found at the site during excavations in 1987.

(31) Belyakovsko Plato (Neolithic and Chalcolithic Settlements)

Popov (1908, 1925) reported bird bones from this site.

(32) Kodja-Dermentska Mound (Neolithic)

Popov (1909, 1918) reported bird bones from here.

(33) Golyamo Deltchevo (Eneolithic Mound)

Ivanov and Vassilev (1975) reported *Anser anser* (Linnaeus 1758), *Anas platyrhynchos*, *Cygnus* sp., and Aves sp. indeterminate from this site.

(34) Ovcharovo (Chalcolithic Mound)

Vassilev (1985) reported *Anser anser*, *Cygnus* sp., *Anas platyrhynchos*, *Tetrao urogallus* Linnaeus 1758, and Aves sp. indeterminate from this site.

(35) Metcha Dupka Cave

Fifteen specimens of passeriforms were collected here in 1981.

(36) Morovitsa Cave

Perdix perdix, *Pyrrhocorax graculus*, and *Coturnix coturnix* (Linnaeus 1758).

(37) Cherdzhenitsa Cave (Eneolithic)

Fifty-eight identifiable bird bones were collected here in 1985.

(38) Giva Laka Cave

Two passeriform specimens were collected here in 1983.

(39) Orehite Locality

Three identifiable bones of small birds.

(40) Brashlyansky Dol Locality (Rock Crevices)

Four fragments of bird bones were found here in 1982.

(41) Chelopech (Neolithic)

Dennel (1978) reported six unidentified bird bones from this site.

CONCLUSIONS

It is clear from this review that data on the origins of the Bulgarian avifauna are few. The oldest fossil bird remains are from the Miocene, and these are incompletely studied. Data on Quaternary birds are more abundant, with 21 species known from the Pleistocene and 14 from the Holocene.

The discoveries of *Lagopus mutus*, *Tetrao tetrix*, *Pyrrhocorax pyrrhocorax*, and *Turdus ruficollis* are of interest in that the first three species have disappeared from Bulgaria, and the first two from the Balkan Peninsula. *Pyrrhocorax pyrrhocorax* is still widespread in the north of Greece, whereas *T. rufficollis* is a very rare visitor to Bulgaria, only having been recorded twice. These species are inhabitants of mountain boreal climatic zones, with the partial exception of *P. pyrrhocorax*, and they indicate a more southern distribution of boreal avifaunal components on the Balkans during the Quaternary.

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MESOZOIC AND PALEOGENE BIRDS OF THE USSR AND THEIR PALEOENVIRONMENTS

Lev A. Nessov

ABSTRACT. The Mesozoic and Paleogene bird fossils of the Soviet Union are reviewed, and important, recently discovered specimens are figured. In most instances, bird bone bearing Cretaceous and Paleogene deposits of the USSR formed in near-shore portions of estuaries and ocean bays adjoining forested coastal plains. Upwelling processes and biological concentration of phosphates caused increased biological productivity in these nearshore waters and resulted in large concentrations of phosphate ions in the waters and sediments, which helped protect small bird bones from dissolution. The diversity of birds appears to have been the greatest in periods of warmer temperatures. The Coniacian assemblage of vertebrates, birds included, is the most diverse among those known from the Upper Cretaceous of Eurasia. A majority of this assemblage originated from a hypothetical, pre-Coniacian, tropical assemblage from southeastern Asia, via an evolutionary process similar in nature to that followed by part of the late Senonian assemblages of North America.

Key words: Aves, Mesozoic, Paleogene, USSR, paleoenvironments.

INTRODUCTION

From 1975 to 1987, the author and his students discovered bones of Cretaceous and Late Paleocene birds in Soviet Middle Asia that were previously unknown from the USSR. During the years 1979–1988, new Eocene and Oligocene localities with bird fossils were discovered. A prediction that any given outcrop in a region would contain Cretaceous bird fossils was usually made after the discovery of fossils of many other rare vertebrates, including amphibians, lizards, pterosaurs, and mammals (Nessov, 1981, 1984, 1987; Nessov and Golovneva, 1987). Only localities with deposits that formed in calm near-shore waters with a high biological productivity, and that contained relatively large numbers of warm climate fossil vertebrates, produced definitive bones of Cretaceous and Paleogene birds. The increase of productivity was connected with upwelling processes that delivered a large concentration of dissolved phosphates from the sea depths into shallow estuaries and bays. These phosphates protected the small remains of birds and other vertebrates from dissolution.

The geologic ages of the Albian to Coniacian, the Late Paleocene, and some Eocene faunal assemblages of the Kyzylkum region were determined by using shark teeth as guide fossils, especially those of Cretaceous anacoracids and Paleogene lamnoids. Jurassic and Santonian–?Campanian localities were dated by using teeth of estuarine sharks, plant fossils, and paleoclimatic data, whereas the early Santonian locality was dated by using brackish water mollusks.

The bird fossils are housed in the Central Museum of Geological Exploration, Leningrad (CMGE), and in osteological collections of the Department of Ornithology of the Zoological Institute of the Academy of Sciences of the USSR, Leningrad (PO).

LOCALITIES

The Mesozoic and Paleogene localities, the bird fossils reported from them and their paleoenvironments are briefly described below. The numbers of the localities correspond to those used in Fig. 1.

1. Upper Jurassic (Upper Callovian?–Kimmeridgian). **Aulije (=Michailovka) locality:** Shales of Karabastau Formation, Karatau Ridge, southern Kazakhstan.

A feather-like object from this locality was described as *Praeornis sharovi* Rautian 1978, which served as the basis for a new subclass of birds, the Praeornithes (Rautian, 1978), characterized by the absence of barbs of the II order. Bock (1986) stated that *Praeornis* was more similar to the pinnate leaf of a cycad than to an avian feather. Paleobotanist A.T. Burakova, Leningrad University, and the author found that the monograph on the Late Jurassic flora of Karatau (Doludenko and Orlovskaya, 1976:pl. 68) has the photograph of a leaf of the same cycad species, *Cycadites saportae* Seward 1895, that was the basis for the description of *Praeornis*. Burakova has also found very similar fossils quite often among other plant material in Bajocian (Middle Jurassic) of Tuarkyr Ridge in Turkmen SSR and Kugitang Ridge in Tadzhik SSR (pers. comm.). It appears that *Praeornis sharovi* is not a bird, but a junior synonym of the cycad *Cycadites saportae.*

2. Lower Cretaceous (Neocomian). **Baissa locality:** Estuarine deposits of the Turga Formation, on the Vitim River, 40 km downstream from the Ust' Zaza meteorological station and approximately 100 km upstream from Romanovka settlement, Lake Baikal region, Burjat Autonomous SSR.

Specimens include feather imprints of various sizes, some of which have the color pattern preserved (Kurochkin, 1985:fig. 42). The fossil assemblage also includes plants and insects.

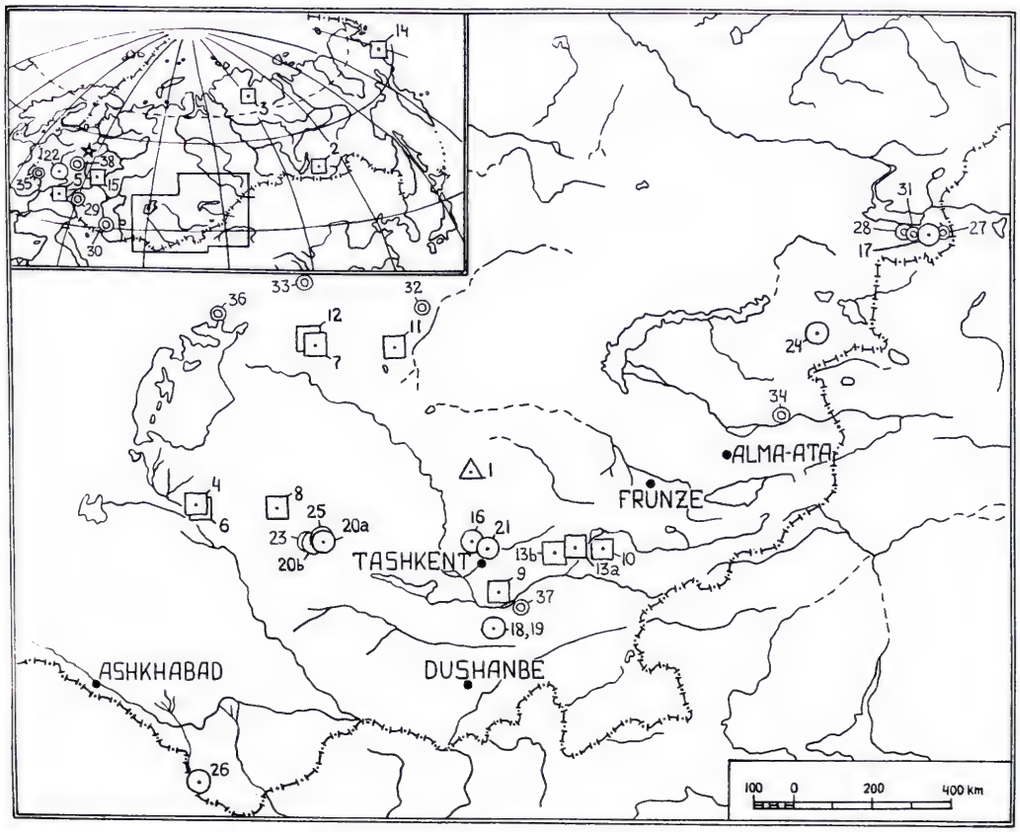

Figure 1. Map showing localities for Mesozoic and Paleogene birds of the USSR (numbers of localities on map and in text correspond). Jurassic (△): **1,** Aulije (=Michailovka). Cretaceous (⊡): **2,** Baissa; **3,** Jantardakh (Hatanga); **4,** Khodzhakul; **5,** Tete-Oba; **6,** Sheikhdzheili and others; **7,** Tjulkeli; **8,** Dzhyrakuduk; **9,** Kansay; **10,** Arslanbob; **11,** Taldysay; **12,** Baybishe; **13a,** Dzhidasay; **13b,** Shakaptar; **14,** Kakanaut; **15,** Malaja Ivanovka. Paleocene and Eocene (⊙): **16,** Zhylga; **17,** Kalmakpay; **18,** Andarak I; **19,** Andarak II; **20a,** Dzheroy I; **20b,** Tashkura; **21,** Maysk; **22,** Kiev; **23,** Daugyz; **24,** Andreyevka; **25,** Dzheroy II; **26,** Joroylanduz. Oligocene (◎): **27,** Zhongiz-Shoki; **28,** Kusto River and area between the Kusto and Kyzylkain Rivers; **29,** Abadzechskaja; **30,** Perekishkjul; **31,** area with localities Bulkair, Tchaybulak, Akzhar, "Bobrovaja Struja"; **32,** Kyzyl-Kak; **33,** series of localities near Tchelkar-Tengiz; **34,** Aktau; **35,** Vorokhta; **36,** Agyspe; **37,** Khanabad; **38,** Stshigry.

3. Lower Cretaceous (Upper Neocomian?) or Upper Cretaceous. **Jantardakh locality:** Sands of the upper part of the Heta Formation with amber; Maymetsha River in Hatanga River Basin, Dolgan-Nenets Autonomous District of Northern Siberia. Kurochkin (1985) noted this locality among others of the Lower Cretaceous, but V.V. Zherikhin (pers. comm., 1989) stated that the locality may be contemporaneous with layers containing Upper Santonian inoceram mollusks.

Specimens represented include small feathers, mammal hair, and insects.

4. Lower Cretaceous (Upper Albian). **Khodzhakul locality:** Yellowish sandstones in lower or middle part of the Khodzhakul Formation, western part of Sultanuvais Ridge, Karakalpak Autonomous SSR.

From this locality comes the proximal piece of a left tarsometatarsus, the holotype of *Horezmavis eocretacea* Nessov and Borkin 1983 (Fig. 2A–E). Although referred to Aves *incertae sedis*, the specimen has some features of the order Gruiformes *sensu lato* (Nessov and Borkin, 1983). The narrow area in the middle part of the anterior fossa of the specimen was slightly compressed by sediments. *Horezmavis eocretacea* was approximately the size of a modern Moorhen, *Gallinula chloropus* (Linnaeus 1758).

This Cretaceous bird lived near the shore of a large bay that was inhabited by a large number of small gastropods; crabs; crayfish; sharks; holocephalians; lepidotid, gyrodontid, and aspidorhynchid holosteans; teleosts; and plesiosaurs. In shallow freshwater and brackish water lakes and swamps adjoining the bay lived discoglosso-pelobatid frogs, small hadrosaurian dinosaurs, small scapherpetontid salamanders, turtles, and crocodiles. The coastal plain was covered with forests of the Araucariaceae and *Platanus*-like angiosperms and inhabited by ankylosaurs, small theropod dinosaurs, and therian mammals of the family Bobolestidae (Nessov, 1987). The climate was warm and semihumid.

5. Lower Cretaceous. **Tete-Oba locality:** Sandstone in the ravine on the western slope of Tete-Oba Hill near Juzhnoje village, Feodossia region, the Crimea.

The specimen from this locality is a positive imprint, on a slab, of a supposed right leg of a bird with narrow toes. The first toe was very short, the third about 5 cm long. The specimen may represent a bird with ralliform affinities (Zernezky, 1958).

6. Upper Cretaceous (Lower Cenomanian). **Sheikhdzheili, Khodzhakulsay, and Tçelpyk localities:** Yellowish sandstone in upper part of the Khodzhakul Formation, western part of Sultanuvais Ridge, Karakalpak Autonomous SSR.

At these localities, an amphicoelous bird vertebra (Nessov, 1984) and unidentified fragments of small bird bones were bur-

ied in sediments of estuarine origin, along with remains of brackish water sharks, diverse actinopterygians (among which dominated lepidotid and pycnodontid holosteans), about nine species of turtles (Nessov, 1986a), primitive protoceratopsid dinosaurs of the genus *Asiaceratops* Nessov and L. Kaznyshkina 1989, small paralligatorid crocodiles of the genus *Shamosuchus* Mook 1924 (Nessov et al., 1989), proteutherian mammals (Nessov, 1987), and small gastropods referable to *Mathildella* sp. (determination by G.G. Martinson). Angiosperms (Platanaceae) and cypresslike conifers lived near the shoreline. The climate was semihumid.

7. Upper Cretaceous (Upper Turonian–Coniacian). **Tjulkeli (=Kankazgan) locality:** White and gray clays of middle or upper part of the Zhirkindeck Formation, Aral Sea vicinity, Kzyl-Orda District, Kazakhstan.

The specimen from this locality is a small feather 12 mm in width (Shilin, 1977). The bird from which came this feather lived near warm, calm estuaries where angiosperm vegetation dominated the shoreline. The climate was semihumid.

8. Upper Cretaceous (Coniacian). **Dzhyrakuduk locality:** Yellowish sandstones of the middle part of the Bissekty Formation (Nessov, 1990) (total thickness about 103 m), Central Kyzylkum Desert, Navoi District, Uzbekistan. At this locality there are three horizons with disarticulated Coniacian bird fossils: horizon CBI-5a, which is 10 m above the main horizon with bird bones at locality CBI-14, and horizon CBI-4, which is about 15 m below horizon CBI-5a or 5 m below the main horizon at CBI-14. Fragments of bird bones are also found in the Upper Turonian part of this locality, in horizon CDZ-17a, which is 32 m below the main horizon at locality CBI-14 and 26 m above the base of the Bissekty Formation.

The assemblage of birds from the main horizon at CBI-14 is very impressive. One species from the locality is *Ichthyornis maltshevskyi* Nessov 1986 (Ichthyornithidae), with a broad sacrum (Fig. 2F–H) (Nessov, 1986b) about 50 percent larger than the type species of the genus (Marsh, 1880). A smaller species from the same level, *Zhyraornis kashkarovi* Nessov 1984 (Zhyraornithidae, ?Ichthyornithiformes) (Fig. 2I–N), has a narrow sacrum, with some similarity to Eocene *Presbyornis* Wetmore 1926 from Argentina (Howard, 1955) and Senonian *Apatornis* Marsh 1873 from the United States (Marsh, 1880). It is interesting that the two sympatric species mentioned above from the main horizon at CBI-14 had some resemblance in body size and sacral width to the North American pair consisting of *Ichthyornis* Marsh 1872 and *Apatornis* (Marsh, 1880). Bird vertebrae from the main horizon at CBI-14 are amphicoelous, as in the order Ichthyornithiformes, and have lateral depressions on the centra similar to those of ichthyornithiforms and some charadriiforms.

From CBI-14 there are also other small to medium-sized bird fossils that are not referable to *Ichthyornis* or *Zhyraornis*. These include the axis of a long-necked form (Fig. 2O, P), a tarsometatarsus (Fig. 2Q–S), a lateral portion of a braincase with adjoining atlas–axis complex (Nessov, 1986b) (Fig. 2T–V), and a piece of a tibiotarsus (Nessov and Jarkov, 1989) of *Sazavis prisca* Nessov, a new enantiornithiform (subclass Enantiornithes) (Fig. 2W–Y). The latter lacks a supratendinal bridge and has a transversely elongated medial condyle and a narrow lateral condyle (see Walker, 1981; Molnar, 1986). A possibly larger enantiornithiform from CBI-14 is represented by a piece of the proximal end of a tarsometatarsus (Fig. 2Z–BB). The teeth of small birds, a tiny mandible (possibly of an ichthyornithiform) with laterally compressed alveoli, vertebra of *Ichthyornis minusculus* Nessov 1990, proximal part of the lower jaw of a bird the size of a little gull, vertebra of an ichthyornithiform the size of the Common Gull, *Larus ridibundus* Linnaeus 1766, and part of a humerus of a medium-sized bird with strange morphology (possibly a new group of Aves) were all collected from CBI-14 in 1989. These and other bird fossils from other levels at locality CBI-14 and from a new, rich site named CBI-50 are now under study.

The Dzhyrakuduk locality is very important for the information it offers regarding the paleoecology of Cretaceous birds, of which very little is currently known (Elżanowski, 1983; Martin, 1983). Phosphatic silt with amphibian, pterosaur, bird and other bones was deposited in the Dzhyrakuduk region in shallow, calm, warm, brackish waters of fluctuating salinity near the mouths of channels connecting estuaries with neighboring lakes. Swift currents of water coursed through the channels in periods of strong winds, eroding unconsolidated silt containing fossil bones and redepositing the bones in cross-bedded sands. We also found in the siltstone phosphatized Coniacian pelecypods (Trigonioidoidea) with excellently preserved mantles and gills, phosphatized beetles (Hydrophilidae and Curculionidae), crayfish (3 species), teeth of sharks and rays (polyacrodontids with "*Lissodus*"-like teeth, *Myledaphus* Cope 1876, *Ptychotrygon* Jaekel 1894, *Ischyrhiza* Leidy 1856, etc.), the holosteans *Amia* Linnaeus 1766, *Lepisosteus* Lacépède 1803, and *Belonostomus* Agassiz 1834, teleosts of the order Elopiformes, salamanders of the families Scapherpetontidae, Batrachosauroididae, and Albanerpetontidae, and archaic discoglossid-like frogs of the family Pelobatidae. These organisms lived in brackish and freshwater reservoirs, in channels and on the shores. Some of them, especially the young, may have been prey of the birds. In turn, some of the giant ichthyodectiform fishes with large thecodont teeth, e.g., *Aidachar paludalis* Nessov 1981, some brackish water sharks, the mesosuchian paralligatorid crocodile *Shamosuchus borealis* (Efimov 1975), eosuchian crocodiles of the genera *Tadzhikosuchus kizylkumensis* Nessov and Cherepanov 1989 were possible predators of the water birds.

Well-preserved island-like areas of forests from along the shores of channels, lakes, and estuaries occur in various levels of the Bissekty Formation. For example, at approximately the level of horizon CBI-5a, there are groups of hundreds and thousands of iron-manganese concretions formed around vertical tree trunks. Stems (Fig. 3) were about 7–15 cm in diameter, with tree trunks spaced at intervals of 10–40 cm. These dense "forest stands" were probably preserved because of near instantaneous tectonic submergence of shorelines. This can be demonstrated by the presence of traces of ancient underwater cracks and fractures in the sediments.

At the level of the paleosol with the manganese concretions and roots of fossil trees, there occur many imprints of small leaves of *Platanus* sp. cf. *P. pseudoquillelmae* Krasser 1896, which make up more than 90 percent of the fossil leaf sample. There are also leaf imprints of *Laurophillum* sp., *Viburnum* sp., and cf. *Magnolia* sp. (determinations by L.B. Golovneva, Botanical Institute, Leningrad). At a distance from the aforementioned dense stands, there are less dense fossilized conifer forests on pink paleosols that also contain trace fossils of burrowing insects. Some trunks of these silicified conifers had many knotholes and all of them had fallen to the ground. Modern habitats with similar living forests usually have diverse avian assemblages, especially near their fringes.

Dry screening of soft sandstones at some sites near the levels with the aforementioned fossil forest stands yielded rare bones of small birds, some of them the size of modern warblers (*Sylvia* Scopoli 1769) and small thrushes (*Turdus* Linnaeus 1758). I am

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convinced that some of the Coniacian birds of Dzhyrakuduk must have lived in the forests. For example, from horizon CBI-5a came a partial humerus of *Kizylkumavis cretacea* Nessov 1984 (Fig. 4A–C), a bird similar to Alexornithiformes Brodkorb 1976 and Enantiornithes Walker 1981. Similar forms were also found in the main horizon at CBI-14 (e.g., see Fig. 4D, E). In 1989, a synsacrum of a new species of *Zhyraornis* Nessov 1984 (Zhyraornithidae, Ichthyornithiformes), which lived a little later than *Z. kashkarovi,* was found.

A few bird specimens were found in horizon CBI-4, among them a coracoid with a deep, round scapular facet and amphicoelous vertebrae, possibly from an ichthyornithiform. Heterocoelous vertebrae are absent from collections of pre-Campanian bird fossils from Soviet Middle Asia. In Asia, Cretaceous heterocoelous vertebrae are known only from the Maastrichtian of Mongolia (Nessov and Borkin, 1983) (Fig. 4F–J). In the uppermost level of CBI-4, 2 to 3 m below the paleosol with manganese concretions and leaves of the Platanaceae, a distal part of a synsacrum, possibly with affinities to ichthyornithiforms, was found in 1989. This specimen was about the size of a Recent cormorant.

The climate of the nearshore Coniacian habitats of Dzhyrakuduk was warm and semihumid, nearly tropical.

The bird fossils of Dzhyrakuduk are clearly associated with the fossilized bones of juvenile and adult, long-necked, toothless, giant pterosaurs of the family Azhdarchidae (see Nessov, 1984; Padian, 1986). Some of the specimens of these pterosaurs were very young. It is possible that these pterosaurs roosted on nearshore trees as the nearest rocky terrain was probably 50–60 km east of Dzhyrakuduk. Ground nesting for the giant azhdarchid pterosaurs was probably unlikely because the terrestrial paleohabitat of Dzhyrakuduk was inhabited by predatory *Cimolestes*-like mammals (Nessov, 1987) and many small to large theropod dinosaurs, i.e., juvenile and adult dromaeosaurids, *Alectrosaurus* Gilmore 1933, *Paronychodon*-like forms, and possibly small spinosaurids. Perhaps the decrease in pterosaurs during the Cretaceous (see Unwin, 1987) and gigantism of the azhdarchid pterosaurs was caused by increasing competition of their young with small and medium-sized birds of various types.

Many species, genera, or families of late Turonian–Coniacian vertebrates of the coastal plains and estuaries of Kyzylkum region were phylogenetically and ecologically analogous to Campanian–Maastrichtian forms of western North America. Such analogues are present among the previously mentioned chondrichthians, holosteans, and elopiform teleosts; salamanders and frogs; the turtles *Adocus* Cope 1868 and *Trionyx* Geoffroy 1809; lizards of the families Necrosauridae and Xenosauridae; pterosaurs of the family Azhdarchidae; dinosaurs of the families Titanosauridae, Dromaeosauridae, Ankylosauridae, Hadrosauridae, and Ceratopsidae (the first indisputable record of the family in Asia); birds of the orders Ichthyornithiformes and Alexornithiformes; and palaeoryctid and condylarth-like mammals (Estes, 1964; Brodkorb, 1976; Lillegraven et al., 1979; Nessov, 1981, 1984, 1986a, 1986b, 1987; Russell, 1984; Padian, 1984, 1986). This analogy allows us to hypothesize that entire assemblages of vertebrates as parts of ecosystems may diverge after division of a geographic area containing the primary community, or that such parts of ecosystems may migrate as units. Some Asiatic forms of Coniacian vertebrates were more advanced than their North American counterparts of the Campanian–Maastrichtian, e.g., in the scapherpetontid salamanders (Nessov, 1981).

Figure 3. Two fossil (Coniacian) nearshore forest groves exposed by wind deflation. Dzhyrakuduk, Central Kyzylkum Desert, Uzbek SSR.

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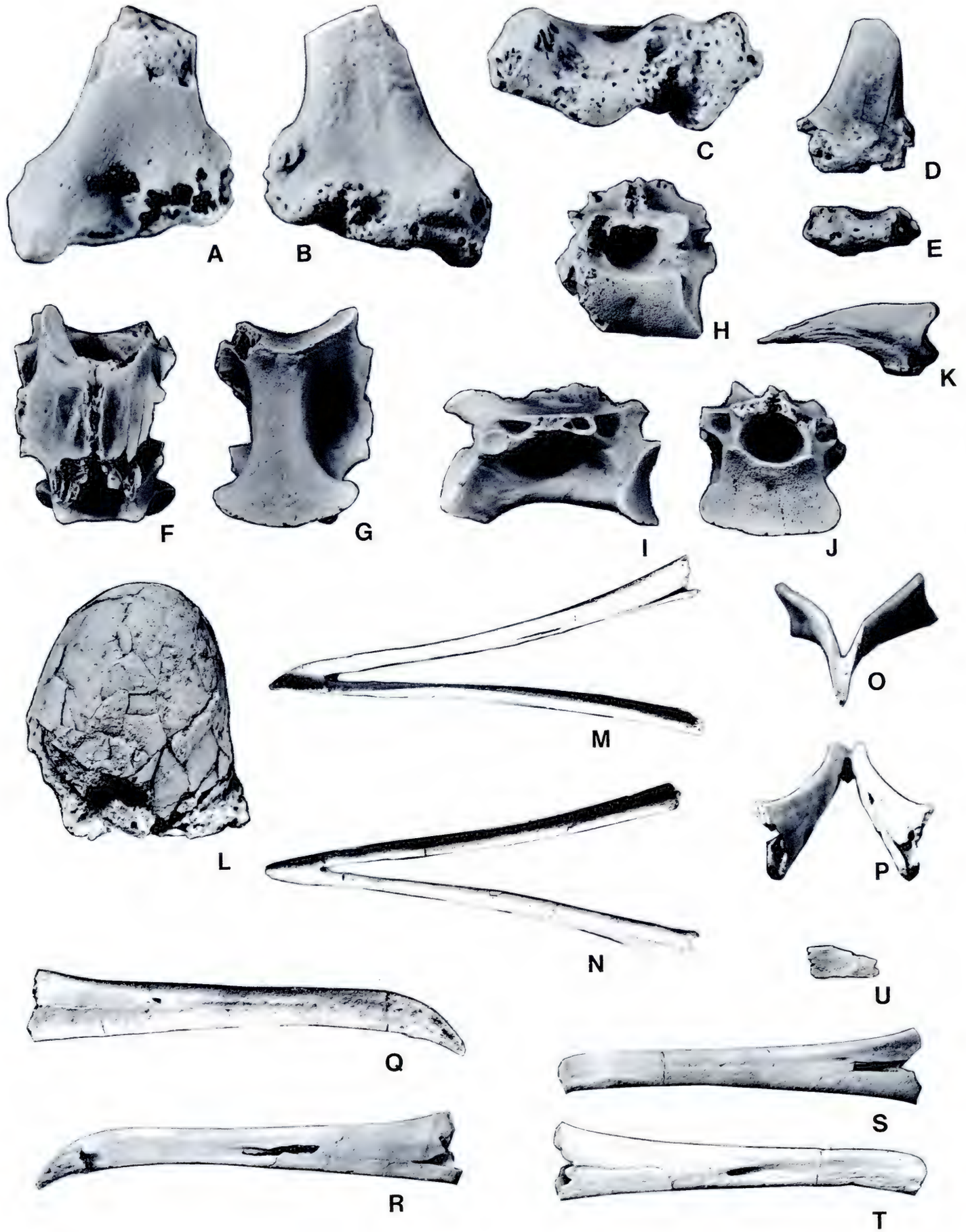
Figure 2. Bird bones of the Cretaceous. Lower Cretaceous, Upper Albian, lower or middle part of the Khodzhakul Formation, Karakalpak Autonomous SSR, Sultanuvais Ridge, Khodzhakul. *Horezmavis eocretacea* Nessov, proximal end of left tarsometatarsus, holotype, PO 3490, in anterior (**A**) and proximal (**B**) views (3×) and posterior (**C**), medial (**D**), and lateral (**E**) views (2.5×). Upper Cretaceous, Coniacian, middle part of the Bissekty Formation, Uzbek SSR, Central Kyzylkum Desert, Dzhyrakuduk. *Ichthyornis maltshevskyi* Nessov, synsacrum, holotype, PO 3434a, in ventral (**F**), and right lateral (**G**) (2.2×), and anterior (**H**) views (3.5×). *Zhyraornis kashkarovi* Nessov, trunk vertebrae, CMGE 43/11915, in posterior (**I**) (6×) and left lateral (**J**) (3×) views; synsacrum, holotype, CMGE 42/11915, in left lateral (**K**) (5×), right lateral (**L**) (3×), and dorsal (**M**) and ventral (**N**) views (2×). Aves indet.; axis, PO 3473, in anterior (**O**) and left lateral views (**P**) (2×); distal end of right tarsometatarus, PO 3434b, in anterior (**Q**) (3×) and posterior (**R**) and distal (**S**) views (4×); and lateral part of a braincase, atlas and axis in phosphate concretion, PO 3434f, in dorsomedial (**T**) and medial (**U**) views, and with atlas and axis in anterior view (**V**) (3×). *Sazavis prisca* Nessov 1989, distal end of right tibiotarsus, holotype, PO 3472, in anterior view (**W**) (2.5×) and medial (**X**) and distal (**Y**) views (3×). Enantiornithes indet.: proximal end of left tarsometatarsus, metatarsal IV broken, PO 3494, in proximal (**Z**), anterior (**AA**), and distal (**BB**) views (3×).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Thus the main lineages of the North American late Senonian vertebrate assemblages could not have originated from the southwestern Asiatic Coniacian fauna, which is the richest known from the Upper Cretaceous of the USSR and Eurasia. It is very likely that both southwestern Asian and American faunas originated from an initial south or southeastern Asiatic fauna, including birds, that inhabited tropical coastal plains and estuaries. It is interesting that the pre-Turonian and post-Coniacian faunas of ancient southwestern Asia differed on generic and familial levels from the late Turonian–Coniacian faunas as well as from the North American Senonian faunas. Perhaps they originated from yet other centers of evolution.

The main changes at the generic and familial level within faunal assemblages coincident with ecosystem alteration in the estuaries and coastal plains of southwestern Asia occurred at the transition from the late Cenomanian to late Turonian, to a lesser degree at the transition from the Coniacian to Santonian, and approximately from the Santonian to Campanian (Nessov and Golovneva, 1987). This suggests that additional research on avian fossils dating from the Cenomanian–early Turonian and the Santonian–Campanian of Central Asia will bring forth much new and important information about previously unknown groups of birds.

9. Upper Cretaceous (Lower Santonian). **Kansay locality:** Red sandstone in upper part of the Jalovatsh Formation, northwestern part of Ferghana Valley, Tadzhikistan.

The specimens of bird fossils from this site are rare fragments from estuarine sediments near the mouth of a paleochannel that possibly connected two brackish reservoirs. The assemblage of sharks, rays, actinopterygians, amphibians, reptiles, and mammals was relatively depauperate (Nessov, 1986a; Nessov and Verzilin, 1983). Abiotic conditions were semiarid, more dry than in the Coniacian, with stronger winds.

10. Upper Cretaceous (Santonian). **Arslanbob locality:** Mixed red clay, sand, and gravel matrix in upper part of Jalovatsh Formation, a cliff in western margin of Arslanbob settlement, northeastern part of Ferghana Depression, Kirghizia.

Smooth eggshells, presumably of birds, were found at this site. The eggshells were about 0.2 mm thick and had an angustocanal microstructure. Sedimentation was subaerial.

11. Upper Cretaceous (Santonian–?Campanian). **Taldysay locality:** Gray clays of the Bostobe Formation, Aral Sea vicinity, Kazakhstan.

The avian specimen from this site is a small, asymmetric feather (Shilin and Romanova, 1978:pl. 26, figs. 5–7). The specimen is a little more than 17 mm in length, with a greatest width of about 4.8–5.5 mm. This covert feather, without distinguishing specific characters, is known under the name *Cretaaviculus saysuensis* Bazhanov 1969. The angle between the barbs of the I order and the shaft is about 20 degrees. This bird lived near brackish water inhabited by trigonioidoid pelecypods and small teleosts. Along the shores grew conifers and small-leaf angiosperms in a subtropical, arid climate.

12. Upper Cretaceous (Upper Santonian–Lower Campanian). **Baybishe locality:** Gray sandstones in upper or middle part of the Bostobe Formation, Aral Sea vicinity, Kazakhstan.

From this site we have a small, thin-boned, pneumatized claw (Fig. 4K) that is possibly from a small bird. The remainder of the faunal assemblage, except for the sharks and rays, and the climate this assemblage suggests were similar to those listed under Kansay locality (9).

13. Upper Cretaceous (Lower Campanian). **Dzhidasay (13a) and Shakaptar localities (13b):** Mixed red clay, sand, and gravel matrix in lower part of the Niczkesay Formation; the former near Tashkumyr, northern part of Ferghana Valley, and the latter in the northwestern part of the same depression, Kirghizia.

From the Dzhidasay locality have come several fragments of eggs and a relatively complete egg (Nessov and Kaznyshkin, 1986) (Fig. 4L) with approximate dimensions of 23–37 mm by 48–55 mm. The thickness of the angustocanal eggshell is about 0.15–0.2 mm. These eggs, in their size and micro- and macrostructure, have some similarity with those of *Gobipteryx* Elżanowski 1974 (Elżanowski, 1981) from the Campanian red beds of the Khermeen Tsav locality in Mongolia. The bird-like eggshells and the egg were found in the Ferghana Valley together with ridged shell fragments of elongated eggs about 150 mm long, which were possibly laid by advanced hadrosaurid dinosaurs (Nessov and Kaznyshkin, 1986).

The matrix also contains calcified roots of Cretaceous plants and underground insect pupal chambers. Deposition of egg-bearing sediment at this site occurred via sporadic, seasonal streams near the northern shore of the large, brackish water Ferghana estuary. The climate was semiarid, with seasonal fluctuations in moisture. Perhaps the small eggs from this site were buried in the ground near the end of the wet season near clutches of large hadrosaur eggs (see Horner, 1982).

14. Upper Cretaceous (Middle Maastrichtian). **Kakanaut locality:** Tuffaceous sandstones in upper part of Kakanaut Formation, "Dva Medvedja" Spring, left tributary of the lower reaches of Kakanaut River, Pekulney Lake Basin, Beringovskiy area, Chukotka Autonomous Region, northeastern part of Russia.

From this locality there are bones of presumably medium-sized birds, deposited with leaves of cycadophites, remains of young and adult hadrosaurs, a medium-sized troodontid theropod dinosaur, and remains of small, indeterminate vertebrates.

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Figure 4. Bird fossils from Cretaceous deposits. Upper Cretaceous, Coniacian, middle part of Bissekty Formation, Uzbek SSR, Central Kyzylkum Desert, Dzhyrakuduk. *Kizylkumavis cretacea* Nessov, distal part of right humerus, holotype CMGE 51/11915, in anconal (**A**) and palmar (**B**) views (8×) and distal (**C**) view (10.5×). Alexornithiformes(?) indet., distal end of left humerus, PO 3434c, in palmar (**D**) and distal (**E**) views (3.6×), Upper Cretaceous, Upper Campanian–Lower Maastrichtian, middle part of Nemegt Formation, Mongolian People's Republic, Transaltaic Gobi, Nogon Tsav. *Judinornis nogontsavensis* Nessov and Borkin, bird, possibly of baptornithid affinities, trunk vertebrate, holotype, PO 3389, in dorsal (**F**), ventral (**G**), anterior (**H**), left lateral (**I**), and posterior (**J**) views (2.5×). Upper Cretaceous, Upper Santonian–Lower Campanian, middle or upper part of Bostobe Formation, Kazakh SSR, Aral Sea vicinity, Baybishe. Aves indet. (?), claw phalanx of hindlimb, PO 3475, in lateral view (**K**) (5×). Upper Cretaceous, Campanian, lower part of Niczkesay Formation, Kirghiz SSR, northern Ferghana, Dzhidasay. Egg, supposedly of *Gobipteryx*-like bird, CMGE 2/12231, lateral view of narrow end, which was oriented down in sediment (**L**) (1.5×). Upper Cretaceous, uppermost Maastrichtian, Malaja Ivanovka. *Volgavis marina* Nessov and Jarkov, dentaries and part of surangular, holotype, PO 3638, lower jaws in dorsal (**M**), ventral (**N**), anterior (**O**), and posterior (**P**) views, right jaw with area of symphysis in right (**Q**) and left (**R**) views, left jaw in external (**S**) and internal (**T**) views, upper part of surangular (**U**) (1×).

Figure 5. Bones of Lower Paleogene birds. Lower Paleogene, Upper Paleocene, quartz sands, Kazakh SSR, Tçimkent District, Zhylga. *Eopuffinus kazachstanensis* Nessov, frontals, holotype, PO 3434g, in dorsal (**A**) and left lateral (**B**) views (2×). *Zhylgaia aestiflua* Nessov, proximal end of left humerus, holotype, PO 3468, in palmar (**C**), anconal (**D**), and external (**E**) views (2×); distal end of humerus, possibly the same specimen as PO 3468, in palmar (**F**) and anconal (**G**) views (2×); distal end of humerus, PO 3485, in anconal (**H**) and distal (**I**) views (2×). Strigiformes indet., phalanx, PO 3482, in lateral (**J**) (1×) and dorsal (**K**) views (1.5×). *Tshulia litorea* Nessov, right tarsometatarsus, holotype, PO 3470, in anterior (**L**), posterior (**M**), and medial (**N**) views (2×). Distal end of right ulna, PO 3480, in internal (**O**) and distal (**P**) views (2×). Aves indet., cranial ends of coracoids, PO 3479, in external view (**Q**) (1×); PO 3476, in dorsal view (**R**) (2.5×); PO 3477, in dorsal view (**S**) (4×).

The remains of plants and vertebrates were buried in mud- and sandflow material within a shallow valley in an area with intensive andesito-basaltic ash volcanic eruptions and a temperate, extrahumid climate.

15. Upper Cretaceous (uppermost Maastrichtian). **Malaja Ivanovka locality:** Quartz-glauconite, greenish sands at the level of about 0.3–0.4 m below the contact with yellowish Paleocene sands with gravel and diverse teeth of sharks, village of Malaja Ivanovka, Krasnaja Derevnja Spring in area of Beliy Jar Valley, Berdeja and Don River Basin, Dubovsky Region, Volgograd District.

The jaws of *Volgavis marina* Nessov and Jarkov 1989 (Fig. 4M–U) were found at this locality. This bird was about the size of *Larus marinus* Linnaeus 1758 and in the structure of the jaws shows some similarity to primitive charadriiforms and the family Fregatidae. The bill of this bird of the subfamily Limnofregatinae had a hook oriented downward, which may have facilitated the seizing and grasping of food. Large and giant pterosaurs of the family Azhdarchidae, the last in the history of the order, which lived in the same Campanian–Maastrichtian sea [*Bogolubovia orientalis* (Bogolubov 1914) in the Penza District] and in other regions [*Arambourgiania philadelphiae* (Arambourg 1959) in Jordanie and *Quetzalcoatlus northropi* Lawson 1975 in Texas] were without such a hook. Teeth of undescribed species of sharks of latest Maastrichtian age, of the primitive, peculiar genus of the family Jaekelotodontidae (determination by V.I. Zhelezko, A.A. Jarkov, and V.V. Istshenko), were also found in this deposit. This locality and a large surrounding area was covered by warm or temperate seas in the latest Maastrichtian, except for the territory of the adjacent Dono-Medvedizkaja Grjada Range, which was a small island area.

16. Lower Paleogene (Uppermost Paleocene–Landenian). **Zhylga locality:** Yellowish quartz sands at the bottom of a quarry near Zhylga (=Dzhylga) settlement in the vicinity of Tashkent, Tçimkent District, Kazakhstan.

Various bird bones were found at this site. These include the frontals of *Eopuffinus kazachstanensis* Nessov 1986 (Procellariiformes), with a relatively narrow shelf for the nasal glands (Nessov, 1986b) (Fig. 5A, B), and the bones (Fig. 5C–I) of the charadriiform *Zhylgaia aestiflua* Nessov 1988 (Presbyornithidae?), which are the size of a modern kittiwake (*Rissa* Stephens 1826) and have some similarity to the Graculavidae (Olson and Parris, 1987). The humerus of *Z. aestiflua* has a long pectoral ridge and a deep, large depression of m. brachialis anticus. Also from the site are a phalanx of a relatively large owl (Fig. 5J, K); a short tarsometatarsus of a juvenile of *Tshulia litorea* Nessov 1988 (Aves *incertae sedis*) (Fig. 5L–N), with some ralliform-like features; and an ulna, possibly of an anseriform (Fig. 5O, P) the size of the modern Eurasian wigeon, *Anas penelope* Linnaeus 1758. The size of most of the known birds of Zhylga vary from that of a starling to a goose (Fig. 5Q–S). The largest known bird here was a new odontopterygiform.

The fossil assemblage also includes various sharks, rays, actinopterygians, *Amia*, albulids, centropomids, nigeropheid sea snakes, and archaic eochelyine sea turtles (Nessov, 1986a). There are extremely rare remains of non-marine turtles (trionychids, platysternids, emydids, and testudinids), mammals [small proteutherians, chapattimyid and paramyid rodents, notoungulates the size of small rabbits, and possibly mylodontid xenarthrans and sirenians (Nessov, 1987)]. The climate was semihumid to humid, near tropical. The bottom of the bay and the shoreline were sandy. Near the shore were forests and small freshwater or brackish water bays. Many vertebrates, among them birds, may have died as a result of "red tides" (de Buisonje, 1972), where phytoplankton metabolites are transferred and accumulated from one trophic level to another.

In 1989, A.O. Averjanov and O.R. Potapova found a new Thanetian site, Zhylga II, with an avian carpometacarpus in a small sand quarry 2 km north of the settlement of Zhylga. They also found abraded Late Paleocene bird bones in an old Darbaza sand quarry in the area between Zhylga and Tashkent.

17. Middle Paleogene (Lower to Middle Eocene). **Kalmakpay locality:** Obayla Formation, Kalmakpay River, southern part of Zaissan Depression, eastern Kazakhstan.

This specimen is the distal part of a tibiotarsus of a gruiform, *Progrus turanicus* Bendukidze 1971 (Kurochkin, 1976), that was buried in the northern part of a large central Asiatic lake or in weakly brackish water of an estuary that stretched from the south at a time of subtropical climate.

18. Middle Paleogene (Lower or Middle Eocene). **Andarak I locality:** Carbonate conglomerate of Upper Suzack Beds, southwestern part of Ferghana Depression, Kirghizia.

This specimen is the distal part of a tibiotarsus of the presumed gruiform *Eobalearica tugarinovi* Gureev 1949. This bird must have died near the interface of plains and a large brackish water gulf. The climate was humid, monsoon subtropical.

19. Middle Paleogene (Middle Eocene; Lower Lutetian, after determination of sharks by N.I. Udovitshenko). **Andarak II locality:** Sandstones and gravels in the middle part of the Alay Beds, 3 km north from Andarak I, southwestern part of Ferghana Depression, Kirghizia.

Bird bones, a distal end of humerus and the proximal end of a carpometacarpus, were found at this locality in 1988 by O.R. Potapova and A.O. Averjanov. This material is now under study by O.R. Potapova. The locality contains remains of oysters, sharks, rays, actinopterygian fish and their coprolithes, turtles, lizards, snakes, crocodilians, and mammals. Conditions were nearshore marine, possibly a shallow, warm-water estuary with high productivity.

20. Middle Paleogene (uppermost Middle Eocene). **Dzheroy I (20a) and Tashkura (20b) localities:** Granular phosphorites, Central Kyzylkum Desert, Navoi District, Uzbekistan.

From Dzheroy I came fragments of small birds, whereas from Tashkura came a part of a carpometacarpus of a large gruiform or odontopterygiform *Asiavis phosphatica* Nessov 1986 (Fig. 6A–C). Evidence indicates that the bird died near the shore of a large bay with upwelling and extremely high biological productivity, inhabited by pteropod and gastropod mollusks, foraminifera, sharks, rays, teleosts, turtles, and various snakes.

21. Middle Paleogene (Middle to Upper Eocene). **Maysk locality:** Yellowish quartz sandstones near the quarry Maysk, area near Tçirtçik, at the border of Uzbekistan and Kazakhstan.

From this site are undescribed remains of birds from a rich assemblage of marine vertebrates of the warm, tropical sea (Nessov, 1982). Another site, located 6 km north of Maysk quarry in the wall of an irrigation canal, has produced an assemblage that includes bone fragments of relatively large, possibly flightless birds.

22. Middle Paleogene (Upper Eocene). **Kiev locality:** Blue "clays" of Kiev Formation, in an area of the old "brick factory of Eismann," near Kiev, the Ukraine.

An ulna and a humerus, possibly both from the same bird, were found by A.O. Averjanov in a collection of various fossil vertebrates made by A.S. Rogowich (1873). These remains, first dated as Lower Eocene, were excavated in 1873. The bones were labeled by the hand of A.S. Rogowich as "*Scolopax* sp.," and indeed they are of charadriiform affinity and belong to

Kievornis rogovitshi Averianov, Potapova, and Nessov 1990 (grade Graculavidae). This fossil bird material (Rogowich, 1873: pl. II, figs. 3, 4) was the first Paleogene bird material ever found in the history of paleornithology in the USSR.

From the Upper Eocene of the Baltic region, fossil bird materials include feathers and presumptive small parts of nests in amber from the Pruss Formation (Lambrecht, 1933; Bachofen-Echt, 1949). Some of these specimens may be found inside recent boundaries of the USSR (in Kaliningrad District and Lithuania). According to Bachofen-Echt (1949), some of these feathers have a similarity to those of *Momotus* Brisson 1760 (Coraciiformes), Piciformes, and Passeriformes. The rich assemblage also includes various plant fossils, arthropods, rare worms, and hair of mammals.

23. Middle Paleogene (Upper Eocene). **Daugyz locality:** Greenish-gray aleurolites with small phosphate nodules raised up from a depth of 40 m in a drilling core near Daugyz settlement in the western part of Tashkura Depression, central Kyzylkum Desert.

This level lies more than 60 m above the level with bone of *Asiavis phosphatica* [Dzheroy I locality (20)]. Undeterminable bird bones (Fig. 6D) at this locality were deposited in a sea with intensive upwelling and high biological productivity. The material was passed to the author by geologists L.N. Shavlis and N.N. Shabanina.

24. Middle Paleogene (Upper Eocene). **Andreyevka locality:** Near Andreyevka settlement, Tçinzhaly River, southern Kazakhstan.

The avian specimens from this site are undetermined fragments of bones (Kurochkin, 1976).

25. Middle Paleogene (Upper Eocene). **Dzheroy II locality:** White quartz sandstones in large deflation hollow near the eastern Muruntau-Tamdy road, Central Kyzylkum Desert, Navoi District. The age of this locality is Upper Eocene, as determined stratigraphically by some geologists, but uppermost Middle Eocene as determined by the large shark and ray fauna (N.I. Udovitshenko, Voroshilovgrad Pedagogical Institute, pers. comm.).

The distal part of a tibiotarsus of the presumed gruiform *Zheroia kurochkini* Nessov 1988 (Fig. 6E–J) comes from this site. This bird has some similarities with ralliforms(?) of the family Laornithidae, with graculavids(?), with some archaic Grues (Nessov, 1988), and with *Cygnavus* Lambrecht 1931 of the Cygninae. Other bird fossils include small coracoids and scapulae, which are similar in morphology to some Late Paleocene forms from Zhylga (No. 16 earlier), and some partial mandibles of odontopterygiforms. Other vertebrates from the site include sharks, rays, teleosts of the families Enchodontidae, Albulidae, Blochiidae, Ostracionidae, and Diodontidae, eochelyine and syllomiine(?) sea turtles, large palaeopheine sea snakes and a small serpent, crocodiles, and rodents. The climate at this site appears to have been semihumid to humid tropical.

26. Middle Paleogene (Upper Eocene). **Joroylanduz locality:** Sandstones of the Namaksar Formation (upper part of Turkestan "Beds"), Joroylanduz Depression, southern part of Turkmenia.

At this site are found three-toed footprints of *Charadrius*-sized birds and four-toed marks similar to footprints of *Tringa* Linnaeus 1758, but with the first toe a little longer. Some other four-toed footprints are of the ralliform type. The site was apparently the shore of a shallow marine bay in a subtropical climate with a cover of xerophitic vegetation (Gorelov, 1974).

27. Upper Paleogene (Lower Oligocene). **Zhongiz-Shoki locality:** Middle or upper part of Aksyir Formation, westward from Zhongiz-Shoki Hill, Aksyir River Basin, southeastern part of Zaissan Depression, eastern Kazakhstan.

The distal end of a tibiotarsus of *Cygnavus formosus* Kurochkin 1968 was found in these deposits, along with remains of fishes, turtles, and mammals.

28. Upper Paleogene (Lower Oligocene). **Kusto locality:** Kusto Formation, Kusto River Basin in southern part of Zaissan Depression, eastern Kazakhstan.

The articular surface for digit III of the tarsometatarsus of *Ergilornis* sp. (Ergilornithidae, Gruiformes) (Kurochkin, 1981) was found at this locality. The remains of Middle Oligocene flamingos, ducks, swans, *Cygnopterus* sp., and *Eogrus* sp. were also identified from the Kusto Formation in the area between the Kusto and Kyzylkain Rivers near the Manrak Range (Kurochkin, 1976).

29. Upper Paleogene (Lower Oligocene). **Abadzechskaja locality:** Gray clays of Maykop Formation (Chadum Beds), Abadzechskaja settlement, Belaja River, Adyge Autonomous District, northeastern slope of Caucasus.

The skeleton of the swift *Jungornis tesselatus* Karchu 1988 (Jungornithidae) was found at this locality. This bird is notable for its mosaic of primitive and advanced features (Karchu, 1988). The skeleton was buried with remains of marine teleosts.

30. Upper Paleogene (Middle Oligocene). **Perekishkjul locality:** Gray and brown clays of the upper part of the Maykop Formation, near settlement of Perekishkjul, northwestern part of Apsheron Peninsula near Baku, Azerbaijan.

A skull and mandible approximately 32 cm long of the marine bird *Caspiodontornis kobystanicus* Aslanova and Burczak 1982 (Pseudodontornithidae, Odontopterygiformes), part of a mandible of another specimen of the same species, and bones of other birds (Aslanova and Burchak-Abramowich, 1982) were found at this site in association with remains of fishes, sea turtles, and cetaceans. The fossils were buried in calm water near the shore of the Maykopian marine basin.

In the uppermost layers of this marine locality (Zuramakent and Riki Beds of Maykop Formation) was found part of the skeleton (humerus, radius, parts of ulnae, coracoids, and scapulae) of the Late Oligocene bird *Guguschia nailiae* Aslanova and Burczak 1968 that was identified as a member of the Cygninae (Anseriformes) (Aslanova and Burczak-Abramowicz, 1968).

31. Upper Paleogene (Middle Oligocene). **Bulkair, Tchaybulak, Akzhar, and "Bobrovaja Struja" localities:** This series of localities near Lake Zaissan, eastern Kazakhstan has produced as yet undescribed bird bones (Kurochkin, 1976).

32. Upper Paleogene (Middle Oligocene). **Kyzyl-Kak locality:** Light sands of Betpakdala Formation on the northern border of Kyzyl-Kak, a dry lake in the Sary-Su River area, south–southwest of the city of Dzhezkazgan, central Kazakhstan.

Fragments of bird bones were found at this locality, some of them belonging to the order Podicipediformes, *Aquilavus* sp., the family Gruidae, and small bustards (Kurochkin, 1976).

33. Upper Paleogene (Middle Oligocene?–Miocene). **Tchelkar-Tengiz locality:** Light sands of *Indricotherium* Beds, a series of localities near semi-dried out Lake Tchelkar-Tengiz, Aktjubinsk District, northern Kazakhstan.

"*Agnopterus*" *turgaiensis* Tugarinov 1940 (Agnopterygidae?, Phoenicopteriformes) was described from an unknown site in this area. Distal ends of humeri of *Cygnopterus lambrechti* Kurochkin 1968 (Anatidae) and *Megagallinula harundinea* Kurochkin 1968 (Rallidae) were found in the Kur-Say ravine. The distal end of the ulna of *Somateria* sp. (Anatidae) and the distal end of a humerus of *Limicorallus saiensis* Kurochkin 1968 (Rallidae) were recovered from Myn-Say ravine (Kurochkin, 1968), but *C. lambrechti* might be the junior synonym of "*A.*" *turgaiensis* and the holotype of *L. saiensis* was recognized as a

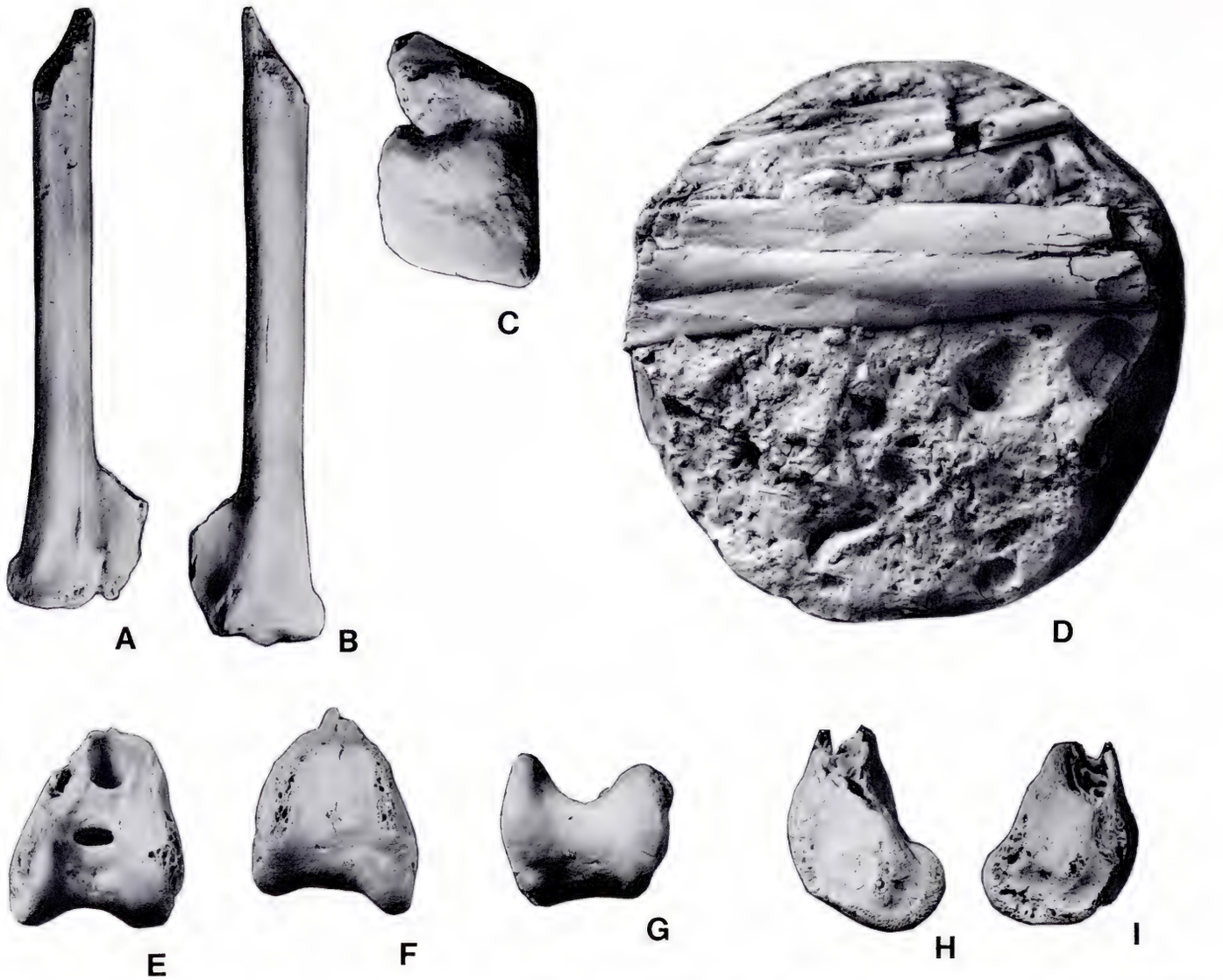

Figure 6. Bones of the Middle Paleogene. Middle Paleogene, Middle Eocene, phosphorite sands, Uzbek SSR, Central Kyzylkum Desert, Tashkura. *Asiavis phosphatica* Nessov, part of left carpometacarpus, holotype, PO 3434h, in lateral (**A**) and medial (**B**) views (1×) and distal (C) (2×). Middle Paleogene, Upper Eocene, unnamed beds, Uzbek SSR, Central Kyzylkum Desert, Daugyz. Aves indet., (**D**) bird bones among phosphate nodules in aleurolites from drilling core, PO 3639; large amount of phosphate material marks ancient process of upwelling. Middle Paleogene, Upper Eocene, quartz sands, Uzbek SSR, Navoi District, Dzheroy II. *Zheroia kurochkini* Nessov, distal part of left tibiotarsus, holotype, PO 3469, in anterior (**E**), posterior (**F**), distal (**G**), medial (**H**), and lateral (**I**) views (1×).

bone of the family Phalacrocoracidae (Mlíkovský and Švec, 1986). These materials were found in 1915 and 1957. Other birds were also identified from Kur-Say and Myn-Say, in Tchelkar-Nura north of Thelkar-Tengiz, including pelecaniforms, several species of the Anatidae (including Cygninae), the Accipitridae, galliforms, gruids, the Fulicinae, and small bustards (Flerov et al., 1974; Kurochkin, 1976). In northeastern Tchelkar-Tengiz, at Donguz-Tau locality, 30 km from Tchelkar-Tengiz, were found the remains of gaviiforms, grebes, ciconiiforms, ibises, and several species of the Anatidae (including members of the Cygninae and Anserinae), Rallidae, Fulicinae, Otididae, and the Charadriiformes. Remains of insects, fishes (including sharks), turtles, crocodiles, and diverse small and large mammals were also found in the previous sites. Habitats in the area must have included damp forests, marshes, and adjoining savannas, all near estuaries.

34. Upper Paleogene? (Middle and Upper Oligocene?–Miocene). **Aktau locality:** Red aleurolites of upper half of the Aktau Formation, Aktau Mountains near Dzhunggar Alatau Ridge, southeastern Kazakhstan.

The distal end of a tarsometatarsus of an ergilornithid (Gruiformes) was found at this site by N.N. Verzilin in 1979, along with remains of emydid, testudinid, and trionychid turtles and mammals.

35. Upper Paleogene or Oligocene. **Vorokkta locality:** Left bank of Prut River, Ivanovo-Frankovskaja District, Ukraine.

The fossil egg of a bird (85.4 mm × 63.5 mm, shell thickness about 1 mm, outline and size similar to eggs of vultures and

Lammergeier) was found at this site (Tsherkatchenko and Ljatchuk, 1960; Dubrovo and Kapelist, 1979).

36. Upper Paleogene? (Upper Oligocene? or Lower Miocene). **Agyspe locality:** Green clays of the upper part of the Aral Formation in the cliffs of the northern coastline of the Aral Sea, western Kazakhstan.

The distal end of a humerus of *Dendrochen oligocena* (Tugarinov 1940) (Anseriformes) and several other undescribed species of the Anatidae (Tugarinov, 1940; Kurochkin, 1976; Mlíkovský and Švec, 1986) and, it seems, one galliform were discovered in these deposits. This nearshore assemblage also includes turtles and mammals.

37. Upper Paleogene? (Oligocene?). **Khanabad locality:** Lower part of Sumsar Beds, near settlement of Khanabad, Isfara (region in Khodzhent Leninabad) District of Tadjikistan.

The distal end of a tibiotarsus of a small bird, teeth of sharks, and a few remains of teleosts were found in this locality by N.I. Udovitshenko. The fossils were buried in the peripheral part of the large, warm Ferghana estuary, where salinity was lower than that in normal seawater.

38. Paleogene? (Oligocene?). **Stshigry locality:** Thin layer of sands above the Cenomanian phosphorite sandstones, in an old quarry near the railroad and station Stshigry, southwestern part of Kursk District, European part of Russia.

Only the diaphyseal parts of small bird bones have been found at this locality.

SUMMARY

A survey of 38 Mesozoic and Paleogene localities, or areas of localities, of the USSR from which avian fossils are known reveals that of the Cretaceous sites, four have produced remains of feathers, eight have produced fossil bird bones, one has yielded a presumed footprint, and three have produced fossil eggs. Twenty-two of the Paleogene localities have produced fossil bird bones, whereas one has produced only footprints, one only a fossil egg, and one region only feathers. The oldest supposed avian record for the USSR, the Upper Jurassic feather-like object described as *Praeornis sharovi,* is recognized as a fossil cycad leaf. Most of the sediments bearing avian fossils were deposited in estuarine or nearshore environments. These deposits often contain a varied assemblage of aquatic marine vertebrates that in some cases can be used as guide fossils to help date the avian fossils.

To the preceding may be added a 1989 discovery by B.V. Prizemlin (Institute of Zoology, Alma-Ata) of some large bird bones (vertebrae, tibiotarsus, and specialized, distinctly flattened tarsometatarsi) that were determined by the author to be remains of an advanced hesperornithiform of a new genus approximately the size of *Hesperornis,* or slightly smaller. The locality is a large quarry 12 km north of the Kushmurun railroad station (Kustanay District of Kazakhstan), in marine phosphorite sands of the lower part of the Zhuravlevo Formation (Upper Campanian–?Lower Maastrichtian). This is the first hesperornithiform to be found in the USSR. This group of birds was originally identified in Asia as the Baptornithidae on the basis of Late Campanian–Early Maastrichtian vertebra of *Judinornis* from Mongolia (Nessov and Borkin, 1983; Nessov, 1986b).

There have also been several new finds of Mesozoic bird feathers not detailed herein from the far eastern USSR (Kara River, Pad' Semjon, Amka River, Arman' River), ranging in age from the Late Jurassic?–Early Cretaceous to the Late Cretaceous (V.V. Zherikhin, pers. comm.).

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